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The Paleoecology and Biogeography of Ordovician Edrioasteroids

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THE PALEOECOLOGY AND BIOGEOGRAPHY OF ORDOVICIAN EDRIOASTEROIDS

A Dissertation Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

René Anne Lewis

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DEDICATION

For my sons,

William Christopher and Richard Wayne Lewis,

you are the loves of my life,

the joys of my heart,

and my gifts to the future.

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ABSTRACT

All organisms are subjected to the biotic and abiotic influences of their surroundings. They derive their energy and essential nutrients from their environment and share their world not only with members of their own species but also with members of other species. Paleoecological analysis uses the fossil record to interpret and reconstruct life habits of past organisms and environments. By examining well-preserved fossil populations we can assess the relationship between the organisms and their surrounding environment, the distribution within their environment, and the nature of their interactions with their environment.

Edrioasteroids, an extinct clade of gregarious, obligate-encrusting echinoderm typical of the Late Ordovician, are rarely encountered in the fossil record because their multi-part skeleton rapidly disarticulates post-mortem. The discovery of large pavements encrusted by nearly completely articulated edrioasteroids therefore indicates that obrution — a sudden input of sediment that smothers the benthic community — occurred. In terms of paleoecological analysis, the near instantaneous nature of obrution results in the examination of a zero-time-averaged census assemblage. By contrast with a time-averaged death assemblage, a zero-time averaged assembly provides a snapshot of the living community at the time of entombment.

This dissertation aims, in three chapters, to increase our understanding of the paleoecology and biogeography of Ordovician edrioasteroids. The first chapter examines a carbonate hardground, collected from the Upper Ordovician strata near Maysville, Kentucky, that is encrusted with four species of isorophid edrioasteroids. Detailed

paleoecologic analyses allows reconstruction of edrioasteroid age structure, thecal orientation, inter- and intraspecific spatial utilization and settlement patterns, and the degree of post-mortem disarticulation. Chapter two examines a brachiopod shell pavement from Florence, Kentucky and a bivalve shell pavement from Sharonville, Ohio in order to investigate the paleoecology of edrioasteroids that colonized these shell pavements. Results are then compared with those from the Maysville hardground. The final chapter of this dissertation summarizes paleogeographic distribution patterns of edrioasteroids during the Ordovician. For this study we collected geographic distribution data from published reports and plotted these occurrences on paleogeographic maps to better predict localities where additional specimens of Ordovician edrioasteroids may be found.

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I. INTRODUCTION

OVERVIEW

Fossils and the sediment in which they are contained reveal information about organism life habits and ancient environments. Paleoecological analysis uses the fossil record to interpret and reconstruct the life habits of past organisms, their association in communities, and their relationship to the environments in which they lived (Brenchley and Harper, 1998). Accurate paleoecological analysis requires knowledge of both organismal functional biology and the taphonomic effects on organismal preservation. In order to maximize potential for retaining paleoecological data, scientists use modern organisms to gain insight on topics such as population structure, community structure, and biogeography of both extinct and extant organisms (Meyer, 1990).

Dodd and Stanton (1990) identify two major focus areas in the study of paleoecology: 1) the interactions between organisms and their environment, which is known as synecology or paleosynecology, and 2) the biological attributes of the individual organism, such as function and lifestyle, which is referred to as autecology or paleoautecology. They suggest that proper ecological reconstruction of ancient environments requires three specific components: 1) a well-established stratigraphic framework in order to best understand the underlying processes in time and space; 2) proper taxonomic identification of fossils, and the correct positioning of the fossils within the stratigraphic framework, and 3) a comprehensive ecologic background that includes an understanding of the ways in which living organisms function within their ecosystem, such as how their morphology and physiology is adaptive to their conditions of life, the

ways in which they interact with one another, and the ways in which they modify their life history to fit the environment.

Isorophid edrioasteroids are an extinct clade of gregarious, obligate-encrusting echinoderms that reached their diversity during the Late Ordovician (Bell, 1976). They are, however, rarely encountered in the fossil record. Their multi-part skeleton consists of several hundred to several thousand ossicles that rapidly disarticulate post-mortem as the soft connective tissue decays (Bell, 1976; Sumrall et al., 2006b). Therefore, the discovery of large pavements containing articulated edrioasteroids indicates that an obrution event had occurred (Brett et al., 1997). Obrution events result from a sudden input of sediment that smothers the benthic community (Seilacher, 1990; Brett and Seilacher, 1991), preserving the community intact. Furthermore, the near instantaneous nature of obrution allows for the examination of a zero-time-averaged census assemblage, allowing for assessment of faunal composition, abundance, diversity, and habitat composition (Brett, 1990; Meyer, 1990; Aguirre and Jiménez, 1997).

Although not always the case, edrioasteroids can be the dominant faunal component when preserved on obrution surfaces (Koch and Strimple, 1968; Bell, 1976; Waddington, 1980; Kammer et al., 1987; Meyer, 1990; Sumrall et al., 2001, 2006a). These occurrences provide an excellent model for discerning paleoecologic patterns of edrioasteroids such as population composition, community structure, and spatial patterns. Currently, the paleoecology of isorophid edrioasteroids is poorly understood for a variety of reasons. Although paleoecologic studies have examined Ordovician edrioasteroids on shells (Meyer, 1990; Sumrall and Zamora, 2011), hardgrounds (Brett and Liddell, 1978;

Waddington, 1980; Guensburg and Sprinkle, 1994), cobbles (Wilson, 1985), and epibiotic associations (Sumrall, 2000; Datillo et al., 2009; Sumrall and Zamora, 2011, in press), in each case the paleoecological settings have been different, and inconsistent methods have been used for assessment. Although methods differ, all studies agree that edrioasteroids require attachment to a hard substrate, whether hardground, shell debris, or other type of firm substrate, and that competition for substrate, a limiting resource, often existed as evidenced by overgrowth and margin deformation (Guensburg, 1988; Meyer, 1990; Sumrall and Sprinkle, 1992; Sumrall, 2001; Sumrall et al., 2006b; Sprinkle and Rodgers, 2010).

Although edrioasteroids have been found throughout the Cincinnatian Series, only two prior studies have focused on their paleoecology (Wilson, 1985; Meyer, 1990). This dissertation examines and compares three edrioasteroid-bearing pavements from the Cincinnati series that each exhibit a different type of hard substrate: 1) the Maysville carbonate Hardground, bearing *Herbertella* brachiopods, three species of bryozoans, and four species of edrioasteroids (Sumrall et al., 2001; Sumrall, 2010; Shroat-Lewis et al., 2011); 2) the Sharonville mollusc shell pavement, bearing multiple encrusters including two species of edrioasteroids, tube worms, and *Zygospira* brachiopods; and 3) the Florence brachiopod pavement, bearing three edrioasteroid species attached to *Rafinesquina* brachiopods (Meyer, 1990). These substrates were chosen for several reasons: 1) they are already in collections, providing access; 2) they come from similar depositional environments; 3) they differ slightly in their associated taxa and the type of attachment substrate; 4) they are nearly coeval, thereby minimizing temporal patterns;

and 5) they bear roughly the same taxa, thereby not confusing autecology with variation in reaction to the substrate.

The geographic distribution of Ordovician edrioasteroids is patchy at best. Although the vast majority of Ordovician edrioasteroid occurrences recorded have been in North America and Europe, this may be a sampling artifact because much of the Ordovician of Gondwana remains unsampled, including: Antarctica, Australia, South America, India, and sub-Saharan Africa (Sumrall and Zamora, 2007). Although Cambrian and Silurian/Devonian edrioasteroids have been found in Australia and other undescribed Cambrian and Silurian edrioasteroids have been found in China and South America, no Ordovician taxa have come forward from these areas. It is likely that a historical lack of paleontological field research may be contributing to our limited understanding of their global dispersal patterns.

This dissertation aims to address the paleoecology and geographic distribution of Ordovician isorophid edrioasteroids. It is divided into parts (II – IV), representing individual research papers, which either are or will be submitted to peer-reviewed journals. This dissertation has been prepared in a style and format consistent with the journal PALAIOS.

Part II – The Maysville Hardground

Since population studies are most reliable when applied to census assemblages, edrioasteroid paleoecology can best be understood by examining catastrophically buried obrution communities. This paleoecologic study examines a carbonate hardground

surface encrusted with four species of isorophid edrioasteroids: *Curvitriordo stecki*, *Carneyella ulrichi*, *Carneyella pilea*, and *Streptaster vorticellatus*.

Encrusting communities smothered by obrution provide samples of *in situ* community remnants (Meyer, 1990; Aguirre and Jiménez, 1997; Brett et al., 1997; Taylor and Wilson, 2003). Because encrusting organisms are cemented to the substrate, they provide direct data on the density, diversity, and spatial relationships within ancient communities. This contrasts sharply with traditional hard substrate assemblages subjected to time averaging, where skeletal remains of non-contemporaneous organisms occur side by side, frustrating attempts to decipher precise ecological relationships (Brett, 1990; Taylor and Wilson, 2003). Nevertheless, in some instances taphonomy strongly suggests that encrusting fossils represent a snapshot of the skeletonized organisms that coexisted at a moment in geologic time (Meyer, 1990).

To draw conclusions about the paleoecology of Ordovician edrioasteroids, we must first understand the relationship that exists between the organisms and their environment. Part II of my dissertation attempts a holistic reconstruction of the edrioasteroid populations and their distributional ecology. This section establishes basic techniques that can be used to assess edrioasteroid paleoecology across all substrate types. Population structure was examined by constructing histograms of maximum thecal diameter. Orientation of the A/P axis of the theca with respect to the substrate was determined by measuring the azimuth of the edrioasteroid A ambulacrum relative to modern true north. The position of ambulacrum A was determined by using either the inherent bilateral symmetry of the oral area, the ambulacral curvature asymmetry, or

position of the anal pore. Spatial distribution upon the substrate was assessed using nearest neighbor analysis, a first-order spatial distribution technique and Ripley's K analysis, which examines spatial distribution at many distance scales. Finally, a new method for determining the degree of edrioasteroid thecal disarticulation was suggested, which uses a progression of seven discrete grades to give insight into postmortem environmental conditions.

Part III – Paleoecologic Comparison of the Florence and Sharonville Shell Pavements

This project further applies the techniques used in Part II to two edrioasteroid-encrusted shell pavements located within the Corryville Formation and Miamitown Shale, found in the Cincinnati, OH area. Suitable attachment substrate on these surfaces is relegated to isolated shells. Consequently they are fundamentally different from the hardground described in Part II where edrioasteroids encrusted a more or less contiguous hard substrate.

The first occurrence, herein referred to as the Florence pavement, was collected from a construction site in Florence, Kentucky, and is currently housed at the University of Cincinnati. Three edrioasteroid species commonly found in the Cincinnatian Series encrust shells on the surface: *Isorophus cincinnatiensis*, *Streptaster vorticellatus*, and *Carneyella pilea*. Edrioasteroids are found attached to shells of the brachiopod *Rafinesquina*.

The second occurrence, herein referred to as the Sharonville pavement, is a mollusc-rich shell pavement from the Upper Ordovician Miamitown Shale studied *in situ* in an educational display at the Trammel Fossil Park, in Sharonville, OH. Two species of

edrioasteroids, *Isorophus cincinnatiensis* and *Carneyella pilea*, are most often found encrusting the common Ordovician bivalves *Ambonychia* and *Modiolopsus*, with fewer examples of encrustation on *Rafinesquina* and *Hebertella* brachiopods, *Loxoplocus* gastropods, and bryozoans. This section discusses the relationship between the edrioasteroids and their selected substrate is examined and its implications. Further, comparisons between the edrioasteroid populations found on the three hard substrates and the paleoecologic implications show both similarities and differences in paleoecology.

Part IV – The Biogeography of Ordovician Edrioasteroids

The final chapter of this dissertation discusses the geographic distribution of Ordovician edrioasteroids. The Ordovician was selected because it is the earliest time where a dense record of edrioasteroids with a global distribution exists. For this study we collected the geographic distribution data for Ordovician edrioasteroids from published faunal reports and plotted these occurrences on paleogeographic maps. This information will help better predict localities where additional specimens of Ordovician edrioasteroids may be found to fill in this record. The compilation of these data helps interpret the distributional patterns in terms of climate, latitude, and ocean currents. Finally, similarity coefficients are used to assess the degree of association of sites where specimens of edrioasteroids have been found.

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II. PALEOECOLOGIC ASSESSMENT OF AN EDRIOASTEROID (ECHINODERMATA)-ENCRUSTED HARDGROUND FROM THE UPPER ORDOVICIAN (MAYSVILLIAN) BELLEVUE MEMBER, MAYSVILLE, KENTUCKY

This chapter is a reformatted version of a paper, by the same name, published in the journal PALAIOS.

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ABSTRACT

Since population studies are most reliable when applied to census assemblages, edrioasteroid paleoecology can best be understood by examining catastrophically buried obrution communities. This paleoecologic study examines a carbonate hardground surface encrusted with four species of isorophid edrioasteroids: *Curvitriordo stecki*, *Carneyella ulrichi*, *Carneyella pilea*, and *Streptaster vorticellatus*. Analysis of edrioasteroid diameters, a proxy for age, shows a bimodal distribution for *Curvitriordo stecki*, suggesting a hiatus in recruitment or multiple spatfalls. Low juvenile mortality may explain a left-skewed distribution among individuals of *Carneyella ulrichi*. Lack of juvenile individuals of *S. vorticellatus* suggests that this population matured from a single spatfall; there were too few specimens of *C. pilea* for analysis. Edrioasteroids on this surface exhibit no preferred ambulacral orientation. Spatial analysis (SA) shows an inter-specific clustered distribution at several spatial scales. Intraspecific SA indicates a clustered distribution for *Curvitriordo stecki* and *Carneyella ulrichi*; there were too few specimens of *S. vorticellatus* and *C. pilea* for analysis. Examination of inter- and intraspecific edrioasteroid taphonomy reveals that thecal collapse, disarticulated cover plates, and disarticulated interambulacral plates occur in nearly half of the population, suggesting brief post-mortem exposure on the paleoseafloor without protection of

sediment cover. Individuals of *S. vorticellatus* suffered thecal collapse, yet all plates and ambulacra remained intact, suggesting that robust thecal elements may inhibit thecal disarticulation.

INTRODUCTION

Encrusting communities smothered on hard substrates by obrution provide samples of *in situ* community remnants (Meyer, 1990; Aguirre and Jiménez, 1997; Brett et al., 1997; Taylor and Wilson, 2003). Because encrusting organisms are cemented to the substrate, they provide direct data on the density, diversity, and spatial relationships within ancient communities. Hard substrate assemblages can be subject to time averaging, such that skeletal remains of non-contemporaneous organisms may occur side by side, potentially frustrating attempts to decipher precise ecological relationships (Brett, 1990; Work et al., 1999; Taylor and Wilson, 2003). Nevertheless, in some instances taphonomy strongly suggests that encrusting fossils represent a snapshot of the skeletonized organisms that coexisted at a moment in geologic time (Meyer, 1990). Articulated multi-element skeletons of echinoderms, such as those described herein, provide testament to sudden and permanent *in situ* burial of a living assemblage. Such census samples may be used to elucidate aspects of paleobiology, such as population structure and spatial positioning of individuals, with great clarity. In turn, data on populations feed into a better understanding of ancient organismal behavior and reproductive strategies.

In the late 1990s, a carbonate hardground was collected from the Bellevue Member of the Grant Lake Formation (Upper Ordovician, Maysvillian) near Maysville,

Kentucky (Sumrall et al., 2001). This hardground (Fig. II-1) was encrusted by a population of 257 isorophid edrioasteroids including four species (Sumrall et al., 2001; Sumrall, 2010): *Carneyella ulrichi* Bassler and Shideler, in Bassler, 1936 (N=125), *Curvitriordo stecki* Sumrall, 2010 (N=121), *Streptaster vorticellatus* (Hall, 1866) (N=9), and *Carneyella pilea* (Hall, 1866) (N=2) (Fig. II-2). The majority of edrioasteroids are attached to the hardground and to bryozoans, although several small edrioasteroids were found attached to brachiopods in life position (Table II-1). Much of the hardground is devoid of encrusting edrioasteroids, suggesting that it was unsuitable for colonization. It is likely that a blanket of mud covered this unoccupied area much of the time (Sumrall et al., 2001). Attachment in such areas would not have been ideal for edrioasteroids, as the fine sediment could clog the respiratory and feeding structures, or not provide the hard substrate that these obligate hard-substrate encrusters need.

Other faunal elements in the terminal community include cyclostome and trepostome bryozoans, the brachiopods *Hebertella*, *Platystrophia*, and *Petrocrania*, annelid worms, *Cornulites* tubeworms, and the crinoid *Cincinnaticrinus* sp. (Sumrall, 2010). Because this hardground was collected in its entirety, it provides an opportunity to study edrioasteroid paleoecology in great detail, allowing the interpretation of edrioasteroid life mode, species associations, and overall community dynamics.

The aim of this study is to evaluate isorophid edrioasteroid paleoecology as reflected by the Maysville hardground. We examined the edrioasteroid age structure, thecal orientation, inter- and intraspecific spatial utilization and settlement patterns, and degree of post-mortem disarticulation. Our null hypotheses were that: 1) population

structure would be consistent across taxa with evidence of multiple generations for each species; 2) a preferred thecal orientation would exist in order to prevent fouling of the oral area; 3) both inter- and intraspecific settlement sites would be clustered upon the hardground to promote reproductive success; 4) spatial analysis would show that settlement patterns were scale independent; and 5) rapid burial by obrution would standardize the degree of post-mortem disarticulation across species for all specimens on the hardground.

Isorophid edrioasteroids, an extinct clade of gregarious, obligate-encrusting echinoderms typical of the Late Ordovician (Bell, 1976), are rarely encountered in the fossil record. Their multi-part skeleton consists of several hundred to several thousand ossicles that rapidly disarticulate post-mortem as the soft connective tissue decays (Bell, 1976; Sumrall et al., 2006b). Therefore, the discovery of large pavements containing articulated edrioasteroids indicates that an obrution event occurred (Brett et al., 1997). Such obrution events result from a sudden input of sediment that smothers the benthic community (Seilacher, 1990; Brett and Seilacher, 1991), preserving the community intact, and allowing for assessment of faunal composition, abundance, diversity, and habitat composition (Aguirre and Jiménez, 1997). The near instantaneous nature of obrution allows for the examination of a zero-time-averaged census assemblage rather than a time-averaged death assemblage (Brett, 1990; Meyer, 1990; Aguirre and Jiménez, 1997). Although these fossil accumulations often preserve fully articulated organisms in life position without the mixing of organisms from subsequent assemblages, minor

disarticulation may occur, indicating some post-mortem decay prior to final entombment (Brett, 1990).

When preserved on obrution surfaces, edrioasteroids can be the dominant faunal component (Koch and Strimple, 1968; Bell, 1976; Waddington, 1980; Kammer et al., 1987; Meyer, 1990; Sumrall et al., 2001, 2006a), thereby providing an excellent model for discerning paleoecologic patterns of edrioasteroids such as population composition, community structure, and spatial patterns. Currently, the paleoecology of isorophid edrioasteroids is poorly understood for a variety of reasons. Paleoecologic studies have examined Ordovician edrioasteroids on shells (Meyer, 1990; Sumrall and Zamora, 2011), hardgrounds (Brett and Liddell, 1978; Waddington, 1980; Guensburg and Sprinkle, 1994), cobbles (Wilson, 1985), and epibiotic associations (Sumrall, 2000; Datillo et al., 2009; Sumrall and Zamora, 2011, in press). In each case, however, the paleoecological settings have been different and inconsistent methods have been used for assessment. Although differences exist, all studies agree that edrioasteroids require attachment to a hard substrate, whether hardground, shell debris, or other type of firm substrate, and that competition for substrate, a limiting resource, existed as evidenced by overgrowth and margin deformation (Guensburg, 1988; Meyer, 1990; Sumrall and Sprinkle, 1992; Sumrall, 2001; Sumrall et al., 2006b; Sprinkle and Rodgers, 2010). Although edrioasteroids have been found throughout the Cincinnatian Series, only two studies have focused on their paleoecology (Wilson, 1985; Meyer, 1990).

Rates of decay and disarticulation have been examined extensively for echinoderms (Meyer, 1971; Liddell, 1975; Kidwell and Baumiller, 1990; Allison and

Briggs, 1991; Brett, 1990; Brett et al., 1997; Nebelsick, 2004; Twitchett et al., 2005). External conditions, such as rate of burial and temperature, factor heavily into the potential for preservation (Kidwell and Baumiller, 1990; Brett et al., 1997) with rapid burial being an essential ingredient for articulated specimen preservation (Bell, 1976; Smith, 1983; Brett et al., 1997; Sumrall and Parsley, 2003; Sumrall et al., 2006b). Although numerous taphonomic scales have been utilized to describe the degree of echinoderm disarticulation in different clades (Brandt, 1989; Twitchett et al., 2005), to date a scale assessing edrioasteroid taphonomic grade has not been proposed. Since degree of disarticulation is qualitative, it is important to determine specific levels for equivalent assessment.

GEOLOGIC SETTING

The Cincinnatian Series is a structurally undeformed sequence of interbedded fossiliferous limestones and poorly fossiliferous shales exposed in the tri-state area of Indiana, Ohio, and Kentucky (Tobin, 1986). These rocks were deposited at approximately 15°–25° S paleolatitude, an ideal setting for the formation of carbonate platforms, and rotated 45° clockwise of present-day orientation (Scotese and Barrett, 1990; Diekmeyer, 1998). Abundant Ordovician exposures of fossiliferous strata in the Cincinnati area have provided a wealth of well-preserved open-marine fossil assemblages. Schumacher (1998) assigned the Upper Ordovician (Maysvillian) Bellevue Member to the Grant Lake Formation. Estimated to be about 446 Ma in age, the Grant Lake Formation grades into shallow subtidal shoal deposits of the Calloway Creek Formation to the south and into irregularly bedded gray, argillaceous limestones interbedded with pavements of

brachiopod shells and shales to the north of Cincinnati, Ohio, USA (Diekmeyer, 1998). Evidence of abundant tempestites has been found in the Bellevue Member indicating that episodic large tropical storms likely occurred (Sumrall et al., 2001). The Bellevue facies was deposited slightly below wavebase (~5–10 m) but with occasional high energy stirring of the sea floor sediments.

In the Upper Ordovician Cincinnatian Series, isorophid edrioasteroids are often encountered on hard substrates such as biogenic shell pavements, bryozoans, and cobbles (Kesling and Mintz, 1960; Meyer, 1990; Dattilo, 1998; Goad et al., 2006; Roberts et al., 2006; Dattilo et al., 2009); however, the Maysville hardground is the only edrioasteroid-bearing carbonate hardground described from the Cincinnati area. Fairly common in the rock record from the Cambrian through the Pleistocene (Taylor and Wilson, 2003), hardgrounds are typically the result of synsedimentarily lithified carbonate seafloors, forming as a result of the supply of calcitic and/or aragonitic cement contained within surrounding seawater from dissolved skeletal material during pauses in sedimentation (Wilson and Palmer, 1992; Wilson et al., 1992).

LOCALITY AND COLLECTION

Collection methods of various edrioasteroid-encrusted substrates have differed. Ideally, the collection of whole sections of encrusted substrate is best for paleoecologic studies, yet to date only two Ordovician edrioasteroid pavements have been collected in their entirety (Meyer, 1990; Sumrall et al., 2001; Sumrall, 2010), including the one described here. This method of collection is rare because large stone pavements are difficult to transport and curate. Most often, edrioasteroids are tightly trimmed of the

extraneous matrix that surrounds prized specimens. In doing so, much of the paleoecologic information, such as faunal and spatial associations and orientation, is lost.

The Maysville hardground (Maysvillian, Upper Ordovician) was collected in 1998–1999 (Sumrall et al., 2001) seven meters above the base of the Bellevue Member of the Grant Lake Formation in a set of roadcuts along State Route 3071 near Maysville, Mason County, Kentucky (Fig. II-1). To aid in reconstruction of the hardground, a map was made using a transparent plastic overlay prior to excavation. Members of the Cincinnati Dry Dredgers, a group of amateur paleontologists, quarried the hardground from the sixth bench of the roadcut under the direction of Sumrall, Brett, and Meyer. The hardground was oriented and cleaned with water and a soft toothbrush to remove loose matrix material (Sumrall et al., 2001; Sumrall, 2010).

The Maysville hardground ranges from 0–10 cm thick and the collected portion covers approximately 10.3 m^2 (Sumrall et al., 2001). Sumrall et al. (2001) closely examined uncollected portions of the hardground for evidence of encrusting edrioasteroids and included these areas on the hardground map, although no edrioasteroids were found on the surface. The hardground surface is irregular on a centimeter scale with evidence of interference ripples (Sumrall et al., 2001).

Lithologically, the hardground is a brachiopod-rich packstone with large valves of *Platystrophia* and *Hebertella* brachiopods. Brachiopod shell debris found near the northern portion of the hardground is likely time averaged as evidenced by a 10:1 brachial:pedicle valve ratio and evident wear on disarticulated shells (Sumrall et al., 2001). In contrast, the presence of fully inflated, articulated, spar-filled brachiopods (Fig.

II-3A) found on the surface in life position indicates that these were live members of the terminal community. Scolecodonts are common in the obrution mud but are small and inconspicuous, averaging a millimeter or two in length (C.R. Fuchs, personal communication, 2001). The high incidence of scolecodonts suggests a lag collection accumulated over an extended period of time. Annulated tubes of *Cornulites*, a probable sedentary annelid worm, are found infrequently encrusting the hardground and brachiopod shells. Encrusting cyclostome and trepostome bryozoans (Fig. II-3B) are sparse over the surface in 1–40 cm wide mounds, with a few projecting several centimeters above the hardground surface. Several bryozoan colonies form uncemented lips over what likely were mud-covered areas of the hardground. In some cases, these projecting portions of the bryozoans were undercut by erosion of soft muds, leaving overhanging exposed ledges. A cryptic fauna composed of three edrioasteroids, a bryozoan, and a *Petrocrania* brachiopod was discovered on the underside of one such bryozoan overhang (Fig. II-4A). *Trypanites*-type borings, commonly associated with bryozoans, were found throughout the hardground (Sumrall et al., 2001). A crinoid holdfast and stem were found attached to a dead and eroded brachiopod on the hardground (Fig. II-4B).

Many edrioasteroids on the surface of the hardground show evidence of burrows circling the perimeter of the theca. In other cases, specimens of edrioasteroids have burrows passing through and disrupting the theca. These burrows suggest that the entombed edrioasteroids were dead and slightly decayed at the time of disturbance (Sumrall et al., 2001).

METHODS

The Maysville edrioasteroid hardground was reassembled almost in its entirety at the Frederick and Amey Geier Collections and Research Center of the Cincinnati Museum Center in Cincinnati, Ohio in 2009. One piece containing two edrioasteroids was missing from the collection. A new map of the hardground noting substrate position of each edrioasteroid was made using a transparent plastic overlay. Edrioasteroids were numbered and data recorded for each specimen including: species name, maximum thecal diameter, orientation of ambulacrum A in relationship to present north, X-Y position on a Euclidian grid, substrate type, and taphonomic grade. Ambulacral width (Fig. II-5) was noted to assess resource partitioning.

Histograms of edrioasteroid maximum thecal diameter were produced to assess population structure. Diameters for incomplete specimens were estimated by doubling radius. Histograms were examined for overall shape and descriptive statistics were calculated.

Thecal orientation on the substrate was determined by measuring the azimuth of the edrioasteroid A ambulacrum relative to true modern north. These measurements were binned into 30° increments for constructing rose diagrams. The position of ambulacrum A was determined by using either the inherent bilateral symmetry of the oral area, the ambulacral curvature asymmetry, or position of the anal pore.

Tests for strength of preferred orientation were conducted using the Rayleigh test for randomness of circular data at the 95% significance level for each species. The R value (Rayleigh's spread), or magnitude is given by:

$$\overline{R} = \frac{\sqrt{\sum \sin\Theta^2 + \sum \cos\Theta^2}}{n}$$

where Θ = mean direction and *n* = number of points. R is tested against a random distribution using Rayleigh's test for directional data (Davis, 2002).

To further our understanding of space utilization, nearest neighbor methods were used to investigate inter- and intraspecific edrioasteroid spatial relationships. Image J software was used to determine area and perimeter of the hardground. X-Y position for each edrioasteroid was determined using the center of the theca.

Two different analyses of spatial distribution were performed using Paleontological Statistics (PAST) software (Hammer et al., 2001). Method one, nearest neighbor analysis (NNA), compares the mean distance between nearest neighbors to the expected mean distance between randomly distributed edrioasteroids. NNA is described as a first-order statistic as it uses one measurement, the distance to the nearest point. This distance is then compared to the expected mean distance assuming a random distribution. The expected mean difference, with correction for map edge effects, is calculated as:

$$\overline{R} = 0.5\sqrt{\frac{A}{n}} + \left[0.051 + \left(\frac{0.412}{\sqrt{n}}\right)\right]\left(\frac{p}{n}\right)$$

where *A* = area of map, *n* = number of points, and *p* = map perimeter (Davis, 2002). The ratio of mean observed to mean expected values (R) measures the departure from a random distribution. An R < 1 represents a clustered distribution, an R = 1 indicates a random distribution and an R > 1 indicates a dispersed distribution. Calculation of the Z statistic determines if the observed pattern varies significantly from a random

distribution. If Z is < –1.96 or > +1.96, we are 95% confident that the edrioasteroids are not randomly distributed (Sumrall et al., 2009).

The second method used, Ripley's K function, analyzes the spatial distribution at many distance scales. Considered a second-order statistic, Ripley's K assesses the complete distribution of all distances in the pattern, comparing local clustering as opposed to general clustering over the area (Ripley, 1976). It assumes the Poisson pattern, i.e., that the points are randomly and independently positioned and that there is no interaction between them (Hammer and Harper, 2006). Nearest neighbor and Ripley's K analyses were conducted on all edrioasteroids on the hardground surface as well as intraspecific examination of *Carneyella ulrichi* and *Curvitriordo stecki*, which occur in sufficient numbers for analysis.

To assess whether areal scale had an effect on the results of NNA or Ripley's K analyses, multi-scale examinations of the hardground were conducted. First, the hardground was arbitrarily divided into three sections of 1.7 m^2, 2.8 m^2, and 5.8 m^2 (Fig. II-6A). Interspecific NNA and Ripley's K analyses were performed on each of these sections. These sections were then further divided in half, resulting in two sections each of 0.85 m^2, 1.4 m^2, and 2.9 m^2 (Fig. II-6B). Interspecific NNA and Ripley's K analyses were performed on each subdivided section. Finally, individual clusters of edrioasteroids were selected (Fig. II-6C) and analyzed using interspecific NNA and Ripley's K analyses.

Substrate preference was noted for each edrioasteroid. Choice of substrate attachment site may provide information about current movement, degree of lithification

of the seafloor, and/or height preference above the substrate. Various substrate preferences were noted, including attachment to the hardground, bryozoans, live brachiopods, and overhangs (Table II-1).

Taphonomic grade can be assigned to isorophids because during death, decay, and burial, edrioasteroid thecae collapse as a result of organic degradation and sediment overburden (Bell, 1976). Generally, the ambulacra and oral plates, which are underlain by the more robust oral frame and floor plates, appear raised, while the thin interambulacral plates are pressed downward against the substrate (Bell, 1976; Sumrall, 2001; Cornell et al., 2003). This process can cause shifting and/or disarticulation of the edrioasteroid plates. The amount and nature of shifting and disarticulation can be assessed using a taphonomic scale. Although numerous taphonomic scales have been utilized to assess the taphonomic grade of extant echinoderms (Brandt, 1989; Kidwell and Baumiller, 1990; Kerr and Twitchett, 2004; Lockwood and Work, 2006), to date a scale assessing edrioasteroid taphonomic grade has not been proposed. Therefore, an empirically designed, semi-quantitative disarticulation scale was devised to evaluate degree of edrioasteroid thecal disarticulation (Table II-2).

A progression of seven discrete grades was chosen to describe degree of disarticulation and taphonomic grade for each edrioasteroid specimen on the hardground was recorded. Edrioasteroids assigned to grade zero are fully articulated with inflation of the theca. Finding a specimen in this condition is highly unlikely, as sediment overburden would cause thecal deflation. Post-mortem deflation and the onset of tissue degradation has occurred in taphonomic grade one (Fig. II-7A); however, no disruption of ambulacral

or interambulacral plates occurred and the oral structure remains fully intact. Taphonomic grade two (Fig. II-7B) is characterized by the disarticulation of the high-relief ambulacral plates as a result of shifting of the theca during deflation. Disarticulation of the flattened interambulacral plates occurs in taphonomic grade three yet the floor plates remain articulated (Fig. II-7C). Often, the more robust peripheral rim remained fully intact although the ambulacral and interambulacral cover plates have disarticulated (Guensburg, 1988). In this case the edrioasteroid is assigned to taphonomic grade four (Fig. II-7D). Taphonomic grade five is assigned if any portion of the peripheral rim is lost (Fig. II-7E). Finally, taphonomic grade six (Fig. II-7F) indicates that the edrioasteroid has undergone some type of bioturbation, such as by worms or other burrowing organisms. Specimens falling into this category receive two scores, one for the amount of thecal disarticulation and another to acknowledge the bioturbation.

RESULTS

The 257 edrioasteroids were dispersed across a total surface area of 10.3 m^2, yielding an overall density of 24 edrioasteroids per m^2. Individually, overall density of *Carneyella ulrichi* was 12.1 individuals per m^2, 11.7 for *Curvitriordo stecki,* 0.8 for *S. vorticellatus*, and 0.2 for *Carneyella pilea* (see also Sumrall, 2010).

Three of the four species of edrioasteroids occur in sufficient numbers to infer population dynamics, and size frequency analyses show variations in distributions between species. Of the 125 specimens of *C. ulrichi*, 108 could be measured for diameter. Size frequency analysis of thecal diameter shows a left-skewed distribution (Fig. II-8A)

with a mean diameter of 20.49 mm (S.D. = 5.87 mm), mode of 16.64 mm, median of 21.23 mm, minimum of 2.5 mm, maximum of 28.75 mm, and skewness of –1.16.

The Maysville hardground contains 121 specimens of *Curvitriordo stecki*, of which 115 could be measured for diameter. Size frequency analysis of the thecal diameters for all measured specimens gives a mean of 16.41 mm (S.D. = 7.35 mm), mode of 13.89 mm, median of 15.99 mm, minimum of 1.0 mm, maximum of 32.03 mm, and a skewness of 0.37. The data show a bimodal distribution representing two distinct subpopulations separated by a 4.9 mm gap (Fig. II-8B). The smaller subpopulation (n=96) has a mean of 13.8 mm (S.D. = 4.83 mm), median of 15.1 mm, and range of 1.00–20.83 mm. The larger subpopulation (n=19) has a mean of 29.49 mm (S.D. = 1.57 mm), median of 29.41, and range of 25.79–32.03 mm. A nonparametric Mann-Whitney U-test was used to determine if the two subpopulations represent samples of the same general population. The U-statistic of 1824 (DF 1 = 96; DF 2 = 19) indicates that these two samples are not representative of the same general population, with a 0.001 level of significance.

Size frequency of the nine specimens of *S. vorticellatus* shows a lack of juvenile individuals (Fig. II-8C) with a mean of 21.26 mm (S.D. = 1.72 mm), median of 20.64 mm, minimum of 19.4 mm, maximum of 24.36 mm, and skewness of 0.98. Caution should be used with analysis of *S. vorticellatus* because of the small population size. Only two specimens of *Carneyella pilea* were found on the hardground with thecal diameters of 20.1 mm and 21.66 mm (Fig. II-8D).

Inter- and intraspecific analyses were conducted to determine if a preferred orientation of the A ambulacrum exists. Of the 257 specimens, 160 could be measured for orientation. Vector analysis of all specimens gave a mean azimuth of 220.53° (Fig. II-9A) and a magnitude of 0.06 with a p value of 0.55, indicating that no preferred orientation existed. Similar results were obtained for the two individual species that occurred in sufficient numbers to infer orientation. For *C. ulrichi*, 98 specimens could be measured for orientation. Vector analysis gave an azimuth of 227.33° (Fig. II-9B) and a magnitude of 0.08 with a p value of 0.51. For *Curvitriordo stecki*, vector analysis of 55 specimens gave an azimuth of 87.17° (Fig. II-9C) and a magnitude of 0.02 with a p-value of 0.95.

X-Y coordinates for 233 specimens could be determined for this study and nearest neighbor for all species revealed a mean distance of 4.4 cm, with an expected mean of random distribution distance of 9.7 cm, a distribution score of R = 0.45, and a Z-statistic of -15.8 ($p < 0.001$), indicating a clustered distribution. Intraspecific NNA analysis reveals that *Carneyella ulrichi* and *Curvitriordo stecki* also showed clustered distributions. *Carneyella ulrichi* had an observed mean distance of 6.7 cm (expected mean = 13.5 cm), distribution score of R = 0.50, and Z statistic of –10.1 ($p < 0.001$). Specimens of *Curvitriordo stecki* had an observed mean distance of 6.9 cm (expected mean = 13.8 cm), distribution score of R = 0.49, and a Z statistic of -10.04 ($p < 0.001$). Specimens of *S. vorticellatus* had a mean distance of 42.3 cm (expected mean = 33.4 cm), distribution score of R = 1.26, and a Z statistic of 1.54 ($p = 0.12$), indicating a dispersed pattern, although these results are based on a small number of individuals. There were too few specimens of *Carneyella pilea* for meaningful analysis.

Inter-and intraspecific spatial patterns were further explored using univariate Ripley's K statistics. Plots of L(d)-d versus distance, where L(d) = the difference between observed pattern and that expected under complete spatial randomness (CSR) and d = distance, show the thicker L(d)-d line lying above the upper 95% confidence interval for CSR for both interspecific analysis of all edrioasteroids (Fig. II-10A) and for intraspecific analysis of *Curvitriordo stecki* (Fig. II-10B), indicating clustering. For *Carneyella ulrichi*, the plot (Fig. II-10C) indicates two different departures from randomness. At very short distances (≤ 2 cm), L(d)-d is less than the 95% confidence level for CSR, indicating a trend towards spatial regularity. At greater distances (≥ 3 cm), however, L(d)-d is larger than 0, indicating spatial clustering. There were too few specimens of *S. vorticellatus* and *C. pilea* for Ripley's K analysis.

To determine if the results of NNA and Ripley's K remain consistent over a variety of areal scales, the hardground was first arbitrarily divided into three sections, as noted above (Fig. II-6A). NNA was conducted on the individual sections using all edrioasteroid specimens within that section. The distribution score in Section 1 is R = 0.65, in Section 2, 0.49, and in Section 3, 0.64 (Fig. II-6A), each indicating a clustered pattern. Ripley's K analysis of each section confirms these findings. These three sections were then each divided in half (Fig. II-6B), creating six sections. NNA indicates that edrioasteroids in Sections 1–5 remain clustered, with distribution scores of R = 0.67, 0.82, 0.62, 0.56, and 0.65 (Fig. II-6B). A distribution score of R = 1.10 in Section 6 indicates that the spacing is random.

Finally, small-scale analysis of individual clusters (Fig. II-6C) was examined using NNA and Ripley's K. Clusters 1, 2, 3, and 5 are randomly distributed (R = 1.13, 1.22, 1.34, and 1.39, respectively), whereas Cluster 4 is clustered (R = 0.85; Fig. II-6C). Although the overall pattern is clustered, random distribution exists within the clusters.

Edrioasteroids were assessed for taphonomic grade using the parameters outlined in Table II-2; none were assigned a grade of zero. Both *Curvitriordo stecki* and *Carneyella ulrichi* show a broad range of grades and appear taphonomically similar to with the majority of specimens receiving a score of five (Figs. II-11A-B). *Curvitriordo stecki* has a mean score of 3.66 and *Carneyella ulrichi,* 3.25. *Streptaster vorticellatus* (Fig. II-11C) has a mean score of 1.62. There were not enough specimens of *S. vorticellatus* and *C. pilea* for statistical analysis.

DISCUSSION

Fossils and the sediment in which they are contained reveal a wealth of information about the life habits of organisms and ancient environments. The Maysville hardground provides us with an exciting and, to date, unique example of an edrioasteroid-encrusted Ordovician hardground from the Cincinnati, Ohio area. The necessity for rapid burial in order to maintain a high degree of thecal articulation assures us that this hardground is not a time-averaged population. The structure of the original skeletonized portion of the community has been preserved in its entirety, allowing for analytical interpretation.

Since two species with closely similar niches cannot stably coexist in the same geographic area (Gause, 1934; Hardin, 1960), the coexistence of the four species of

edrioasteroids on this hardground suggests that some type of specialization likely occurred for dietary needs to be met. Meyer (1979, 1982a, 1982b), and others (Rutman and Fishelson, 1969; Fishelson, 1974; Messing, 1997; Brower, 2006) suggest that ambulacral width on living crinoids dictates the maximum dimension of an ingested food particle. We suggest that differences in the size of edrioasteroid ambulacral food grooves, which extend the length of each ambulacrum, correspond to three different feeding strategies. The wide ambulacral width of *S. vorticellatus* (Fig. II-5A) suggests consumption of larger food particles than in *Carneyella ulrichi* (Fig. II-5B) and *C. pilea* (Fig. II-5C), which have narrower ambulacral widths. *Curvitriordo stecki*, with smaller ambulacral widths (Fig. II-5D), probably consumed the smallest food particles.

Overall density of 24 edrioasteroids per m^2 on the hardground compares to that reported by Meyer (1990) but is much lower than that seen by Sumrall et al. (2006b; 2009) where densities reached a peak of 5000 individuals per m^2. Specimen diameter, a proxy for age, provides an estimate of the age structure of the population at the time of burial. We predicted that edrioasteroid population structure would likely be consistent across taxa; however, the results indicate otherwise. Three of the four species of edrioasteroids occur in sufficient numbers to discuss size frequency. The population of *Carneyella ulrichi* (Fig. II-8A) is strongly left skewed. Similar results were found by Sumrall et al. (2006b), who suggested that left-skewed distributions occur as a result of either low juvenile mortality rate or decreased growth rate as individuals reach maturity. A histogram of *Curvitriordo stecki* (Fig. II-8B) clearly indicates a bimodal distribution (Sumrall, 2010). Weaker bimodal distributions have been found in populations of

Neoisorophusella lanei (Kammer et al., 1987) and *S. vorticellatus* (Meyer, 1990). A bimodal population distribution is likely the result of a recruitment hiatus, multiple spatfalls, or some other factor that led to a lack of larvae recruitment. The tight unimodal distribution of large specimens of *S. vorticellatus* on the hardground is reminiscent of a similar distribution of *Torquerisediscus kypsi* (Sumrall, 2001), which suggests that the population is likely the result of a single spatfall.

We predicted that there would be a preferred orientation of the edrioasteroid theca, with the anus located down current. Our results indicate that no such preferred orientation exists (Fig. II-9). Studies by Sumrall (2001) and Cornell et al. (2003) similarly found no preferred thecal orientation. Roberts et al. (2006), however, found weak thecal orientation in edrioasteroids attached to a bivalve shell pavement, as did Sumrall et al. (2009) for specimens of *Multiplexidiscus mckenziensis*. Smith (1983) showed very strong preferred orientation for 55 specimens of *Leipidodiscus milleri*. These results suggest that: 1) edrioasteroids may have had a method to prevent the occurrence of fouling if the anus was located up current from the mouth; 2) edrioasteroids may have been insensitive to current direction; 3) these edrioasteroids were unable to detect current; 4) the current may not have been strong enough; or 5) the current may not have been consistent enough for detection by the edrioasteroids.

We predicted that both inter- and intraspecific settlement sites would be clustered upon the hardground, giving us insight into edrioasteroid interactions and competition. No inter- or intraspecific interactions, such as margin deformation, are noted between edrioasteroids and other faunal elements on this surface such as those seen in Meyer

(1990), Sumrall et al. (2006b), and Sprinkle and Rodgers (2010). Interspecific analysis indicates that the entire suite of edrioasteroid populations is clustered on the hardground. Intraspecific analysis shows that both *Carneyella ulrichi* and *Curvitriordo stecki* were clustered on the hardground as well, whereas individuals of *S. vorticellatus* were dispersed.

NNA of the hardground edrioasteroids shows a clustered pattern when the slab was arbitrarily divided into three sections (Fig. II-6A); however, when subdivided into six sections (Fig. II-6B) there are changes as a result of area reduction. At this scale the individuals contained within Sections 1–5 (Fig. II-6B) remain clustered, while Section 6 (Fig. II-6B) shows a randomly distributed pattern. Lastly, NNA of the individual clusters (Fig. II-6C) indicates a random distribution with the exception of Cluster 4 (Fig. II-6C), which remains clustered. These findings suggest that at smaller spatial scales, the clustering pattern weakens or disappears. This is potentially a very important result as these smaller scales are closer to the scale where the individual organisms directly interact (or do not interact) with each other. As sessile organisms, it would be essential for the edrioasteroids to be in an area where their nutritional needs were met. Therefore, they may have been clustered in an area where the current provided for increased feeding opportunity.

There was no evidence of antithetic behavior among the edrioasteroid species, suggesting that some other physical factor simultaneously controlled the distribution of species on the hardground. Kammer et al. (1987) suggest that clustering is an indication that suitable substrate for settlement was at a premium. We propose that the irregular

surface on the Maysville hardground was likely heterogeneous, with fine sediment settling in locally low areas. The necessity of a firm substrate for attachment and low turbidity would have precluded settlement by the edrioasteroids on mud. It is possible that some of these areas were colonized but the edrioasteroids did not survive, with disarticulation occurring prior to the obrution event.

Furthermore, reproductive success may have been enhanced as a result of the clustering. Organisms that release gametes into the environment are dependent upon the ability of sperm and eggs to find each other. Levitan et al. (1992) found that the distribution and abundance of spawning organisms is crucial for reproductive success. Fertilization success is known to decline rapidly with distance between individuals and reproductive success increases dramatically if an individual is in the center of a large spawning aggregation.

As previously mentioned, post-mortem preservation of the multipart theca necessitates rapid burial and we predicted that the degree of post-mortem disarticulation would be equal for all specimens. The majority of the populations of *Carneyella ulrichi*, *C. pilea*, and *Curvitriordo stecki* (Fig. II-11A-B), however, were assigned higher taphonomic grades, indicating that thecal collapse and disarticulation of both the cover plates and interambulacral plates occurred. This suggests that brief post-mortem exposure on the seafloor without protection of sediment cover likely existed. On the other hand, specimens of *S. vorticellatus* (Fig. II-11C) were assigned lower taphonomic grades with most fully articulated; the robustness of the thecal plates in this taxon may account for this difference. Burrowing organisms were able to tunnel through the sediment and

disrupt two specimens of *C. stecki*, however, suggesting that the edrioasteroids were dead and partially decayed prior to burrowing, as burrows could not have penetrated live edrioasteroids.

CONCLUSIONS

1. Edrioasteroid population structure across the hardground from the Upper Ordovician Bellevue Member of the Grant Lake Formation varied by species.

2. There was no preferred thecal orientation on the hardground.

3. Interspecific analysis shows that all edrioasteroids are clustered on the hardground.

4. Intraspecific analysis shows that *Carneyella ulrichi* and *Curvitriordo stecki* are clustered on the hardground whereas specimens of *Streptaster vorticellatus* are dispersed.

5. The clustering pattern for all edrioasteroids on the surface weakened or disappeared as reduction of the substrate area occurred.

6. Specimens of *Carneyella pilea, C. ulrichi,* and *Curvitriordo stecki* show a high degree of disarticulation whereas *S. vorticellatus* shows little thecal disarticulation.

7. Edrioasteroid ambulacral diameter suggests partitioning of food supply.

8. Encrusters on the underside of the bryozoan ledge suggest a broader attachment strategy than previously thought.

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APPENDIX II

TABLE II-1 – List of organisms and substrate preferences.

Substrate	Hardground	Bryozoan	Live Brachiopod	Overhang
Species				
Carneyella ulrichi	124	4	2	3
Curvitriordo stecki	108	4	3	0
Streptastar vorticellatus	7	1	0	0
Carneyella pilea	2	0	0	0

TABLE II-2 – Taphonomic grading scale indicating degree of disarticulation.

Grade	Appearance of edrioasteroid theca
0	Fully articulated and complete. Theca inflated.
1	Thecal collapse. All plates and ambulacra intact.
2	Cover plates begin to disarticulate. Shifted disruptions of theca.
3	Interambulacral plates begin to shift.
4	Only peripheral ring remains intact. No coherence with plates, if present.
5	Peripheral ring is incomplete.
6	Bioturbation disturbance present (i.e., worm burrows).

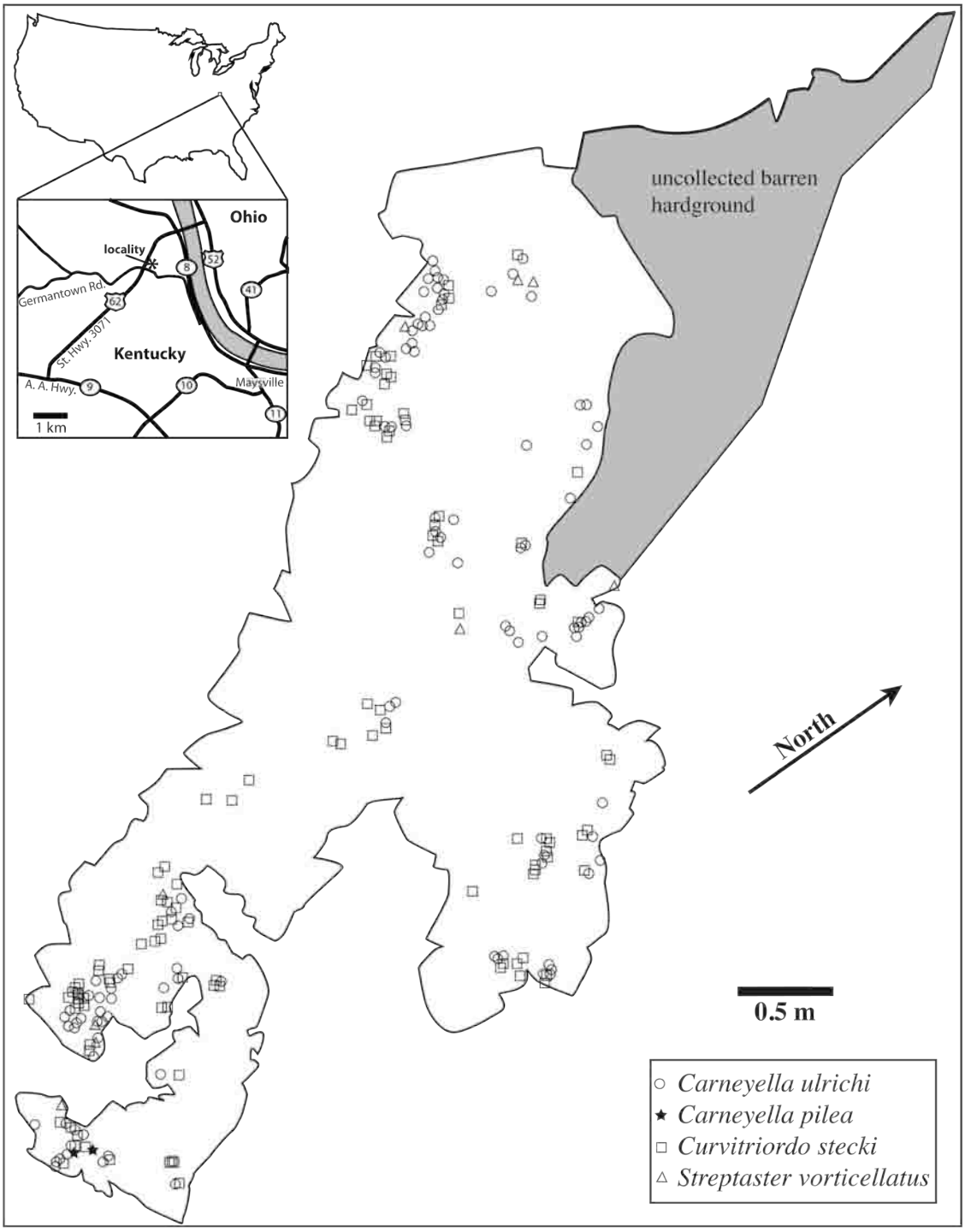

FIGURE II-1 – Map showing location of edrioasteroids on the hardground surface. Edrioasteroids are not randomly distributed on the hardground. Insert shows location map of the locality where the edrioasteroid specimens were collected (after Sumrall, 2010).

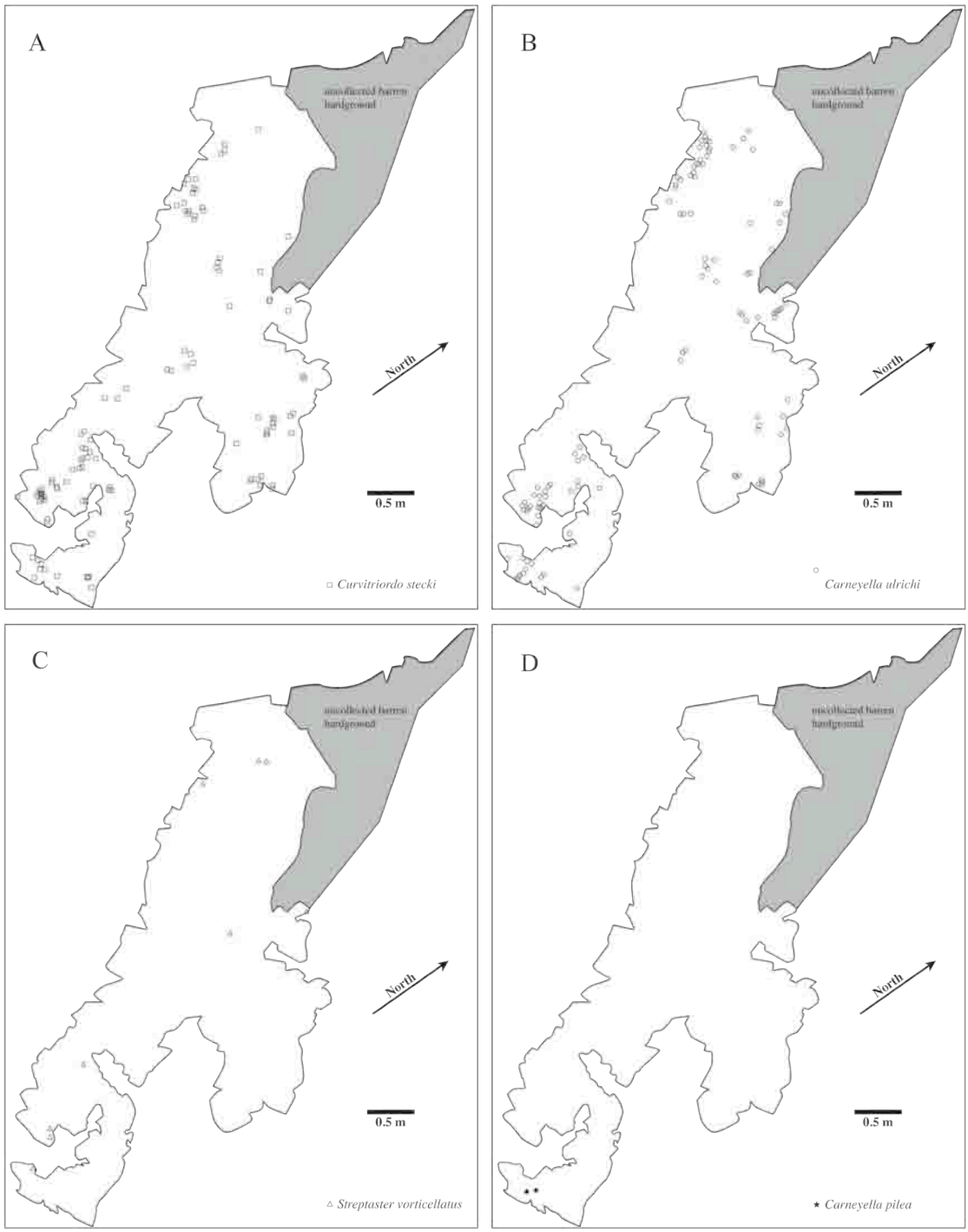

FIGURE II-2 – Map showing location of the four edrioasteroid species on the hardground surface. Specimen density for the observed portion of the hardground is as follows: A) *Carneyella ulrichi*, 12.1 specimens/m^2; B) *Carneyella pilea*, 0.2 specimens/m^2; C) *Curvitriordo stecki*, 11.7 specimens/m^2; and D) *Streptaster vorticellatus*, 0.8 specimens/m^2.

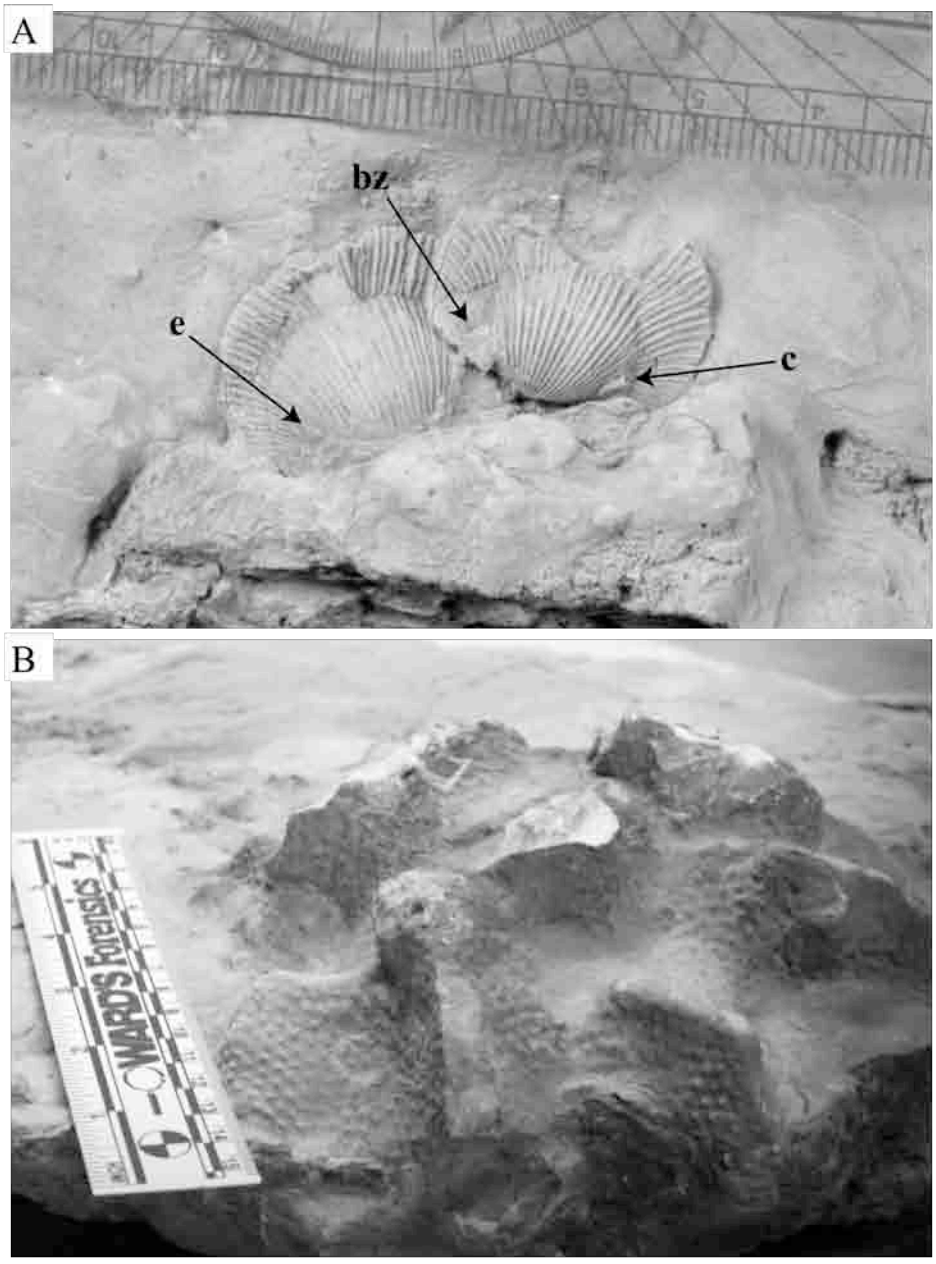

FIGURE II-3 – Typical organisms found on the Maysville hardground. A) Two fully articulated *Herbertella*, spar-filled, attached to large bryozoan with epibiont edrioasteroid, bryozoans, and cornulitids. Abbreviations are: e = edrioasteroid, bz = bryozoan, c = cornulitid. B) Large bryozoan colony found on the hardground.

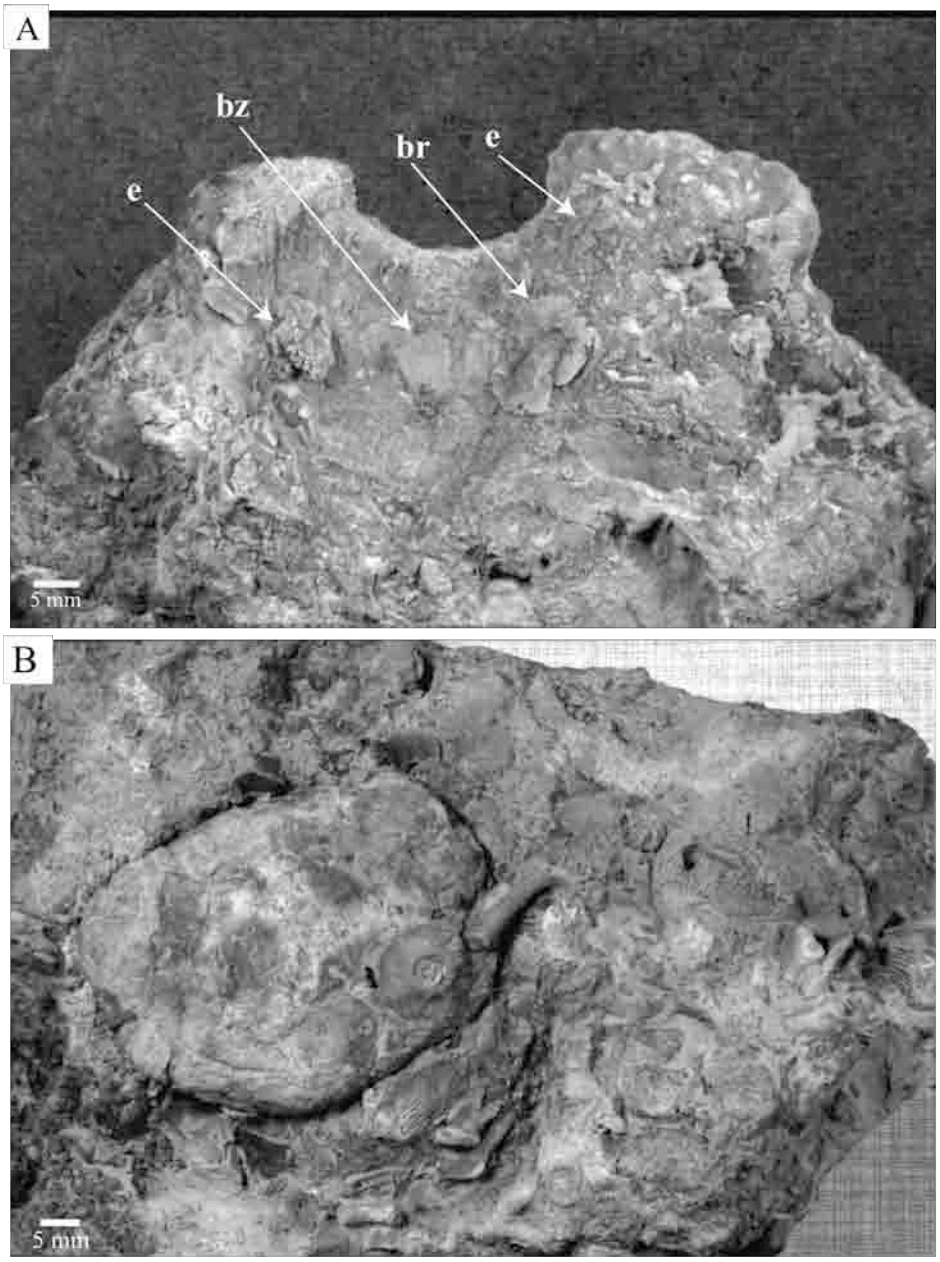

FIGURE II-4 – Typical organisms found on the Maysville hardground.A) Overhang with cryptic fauna. Abbreviations are: e = edrioasteroid, bz = bryozoan, br = brachiopod. B) *Cincinnaticrinus* holdfast and stem on brachiopod.

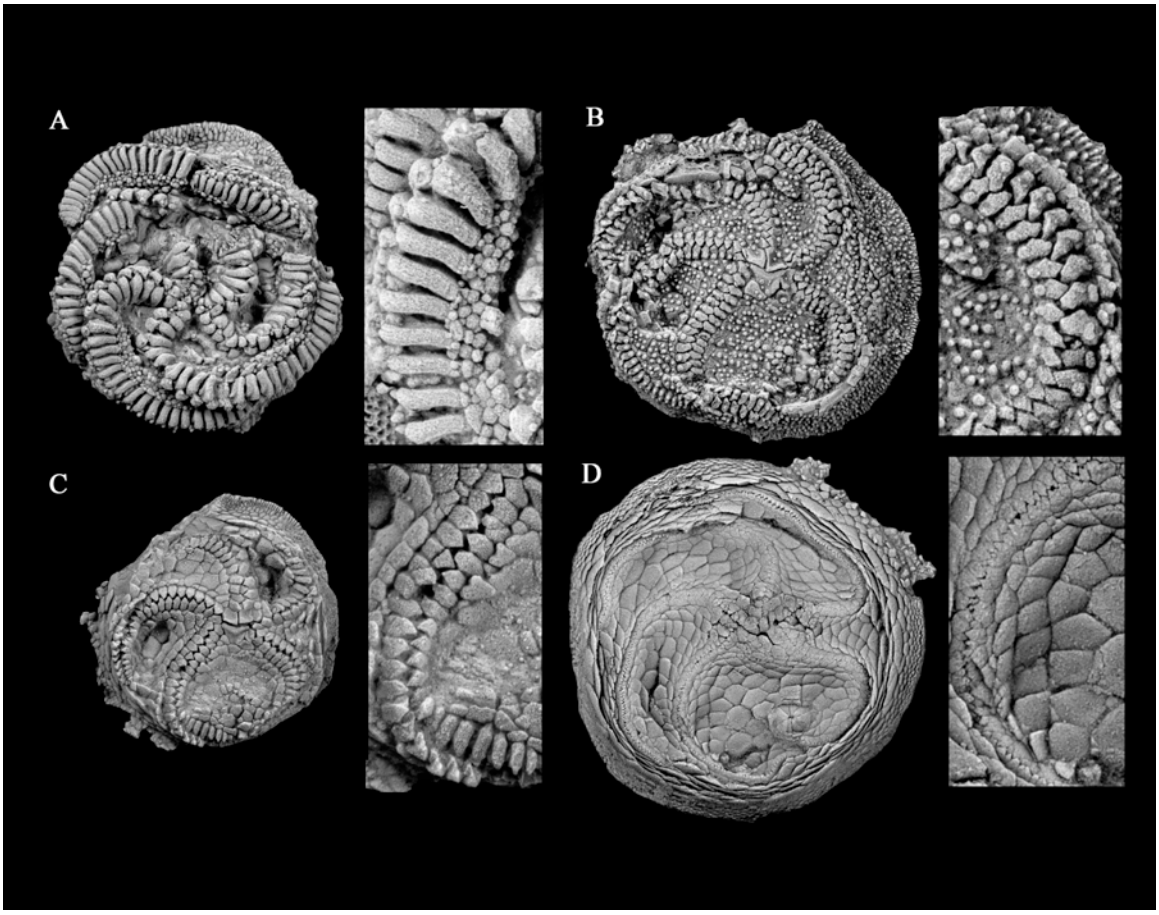

FIGURE II-5 – Ambulacra width suggests size of food particles consumed. A) *Streptaster vorticellatus* with wide ambulacral cover plates, B) *Carneyella ulrichi* C) *Carneyella pilea* with large ambulacral cover plates, and D) *Curvitriordo stecki* with small ambulacral coverplates. All specimens are 2X magnification. Ambulacra are 5X magnification.

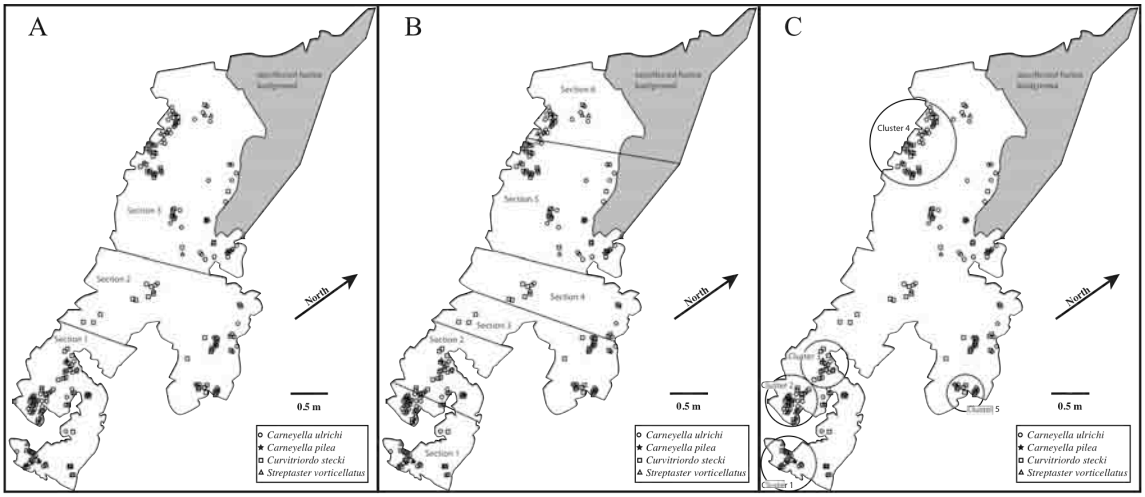

FIGURE II-6 – Spatial distribution of edrioasteroids on the Maysville hardground. A) Division of the Maysville hardground into three sections. Section 1 is 1.7 m^2 with 96 specimens yielding a density of 56.4 specimens/m^2; section 2 is 2.8 m^2 with 47 specimens yielding a density of 16.7 specimens/m^2; and, section 3 is 5.8 m^2 with 90 specimens yielding a density of 15.5 specimens/m^2. B) Division of the Maysville hardground into six sections. Section 1 and 2 measure 0.85 m^2 with 64 and 32 specimens respectively, yielding a density of 75 specimens/m^2 and 37 specimens/m^2. Sections 2 and 3 each measure 1.4 m^2 with 32 and 15 specimens respectively, yielding a density of 22.8 specimens/m^2 and 10.7 specimens/m^2. Sections 5 and 6 measure 2.9 m^2 with 63 and 27 specimens respectively, yielding a density of 21.7 specimens/m^2 and 9.3 specimens/m^2. C) Clusters of edrioasteroids located on the Maysville hardground. NNA on clusters 1, 2, 3, and 5 indicate a random distribution; cluster 4 has a clustered distribution.

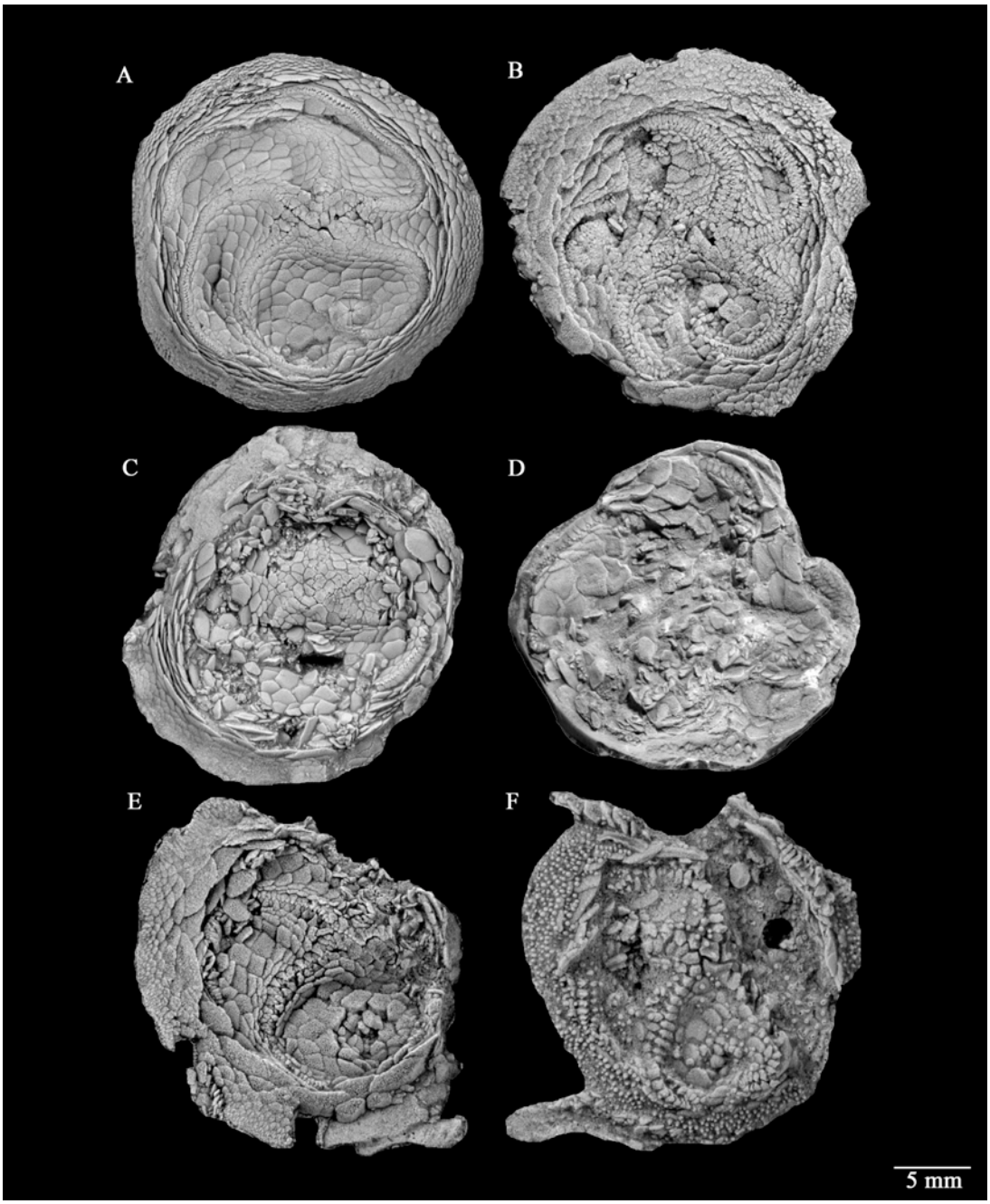

FIGURE II-7 – Edrioasteroids showing various taphonomic grades from the Maysville hardground. A) Grade one; thecal collapse has occurred, but all plates and ambulacra intact. B) Grade two; shifting of ambulacral and cover plates. C) Grade three; interambulacral plates are disarticulated from the theca. D) Grade four; only the peripheral rim remains intact. E) Grade five; peripheral rim is incomplete. F) Grade six; bioturbation disturbance is present in the form of two annelid burrows. The first moves through the right side of theca while the second circles the bottom and exits to the left. A, C-E = *Curvitriordo stecki*; B, F = *Carneyella ulrichi*.

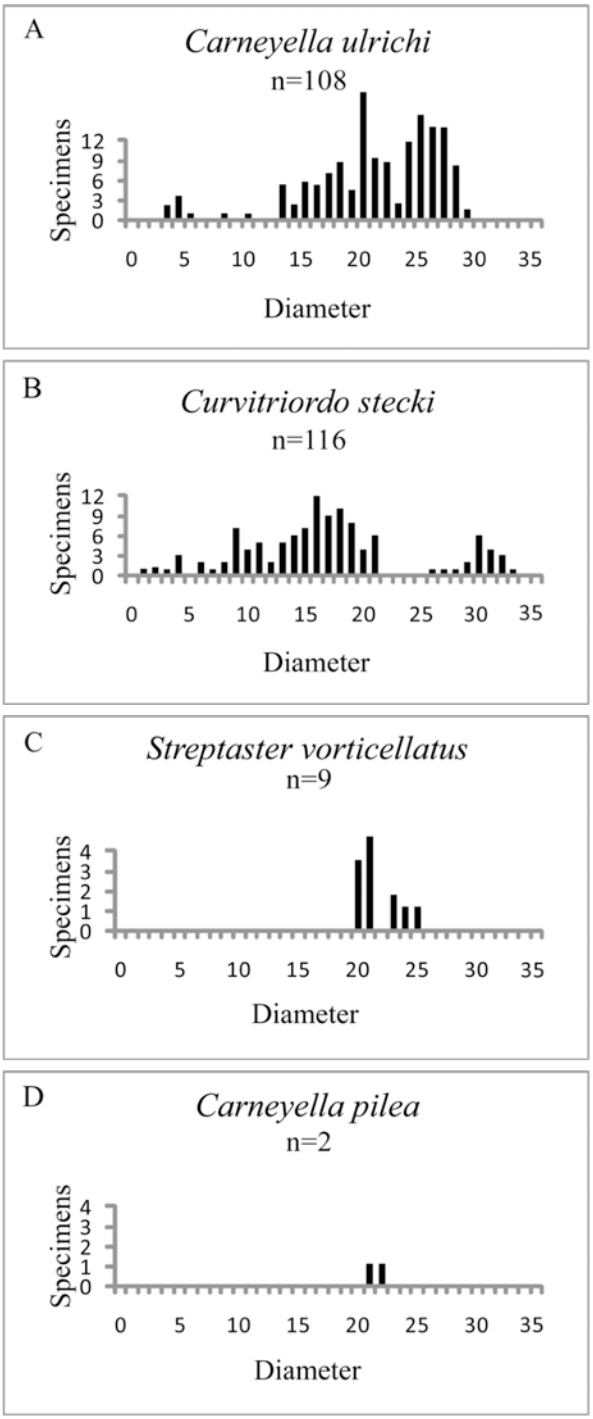

FIGURE II-8 – Histograms showing the frequency distribution of edrioasteroids on the Maysville hardground. A) *Carneyella ulrichi*, a left-skewed population. B) *Curvitriordo stecki*, a bimodal distribution. C) *Streptaster vorticellatus*, a lack of juvenile individuals. D) *Carneyella pilea* showing two mature specimens (after Sumrall, 2010).

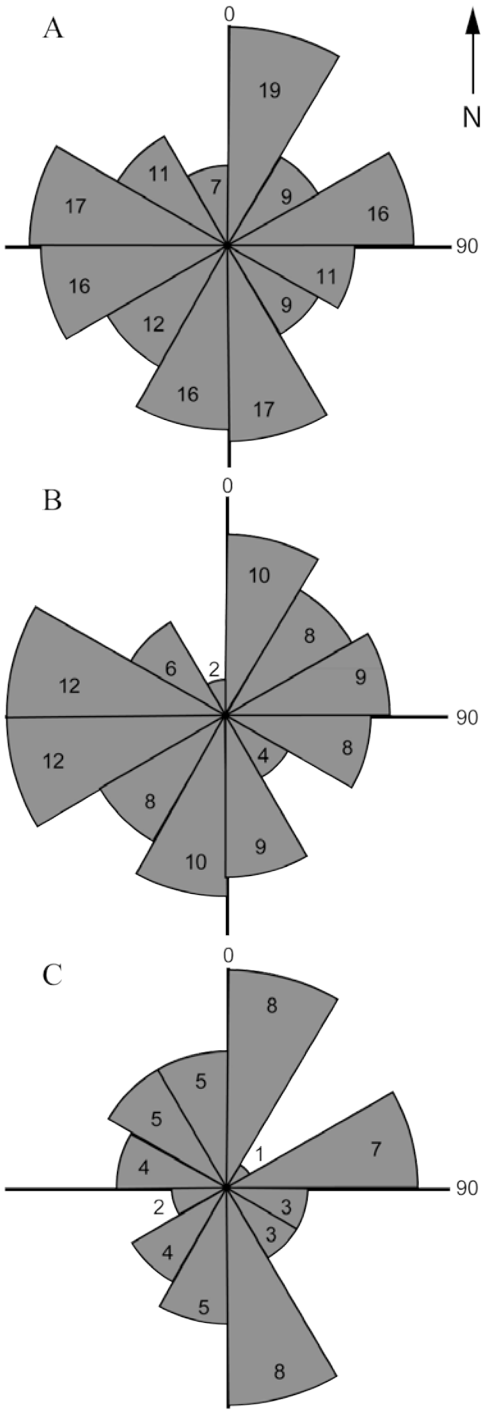

FIGURE II-9 – Orientation of edrioasteroids on the Maysville hardground. Preferential orientation would be expected in order to prevent fouling of the mouth and ambulacra, but all show no preferential orientation. A) All edrioasteroids. B) *Carneyella ulrichi*. C) *Curvitriordo stecki*.

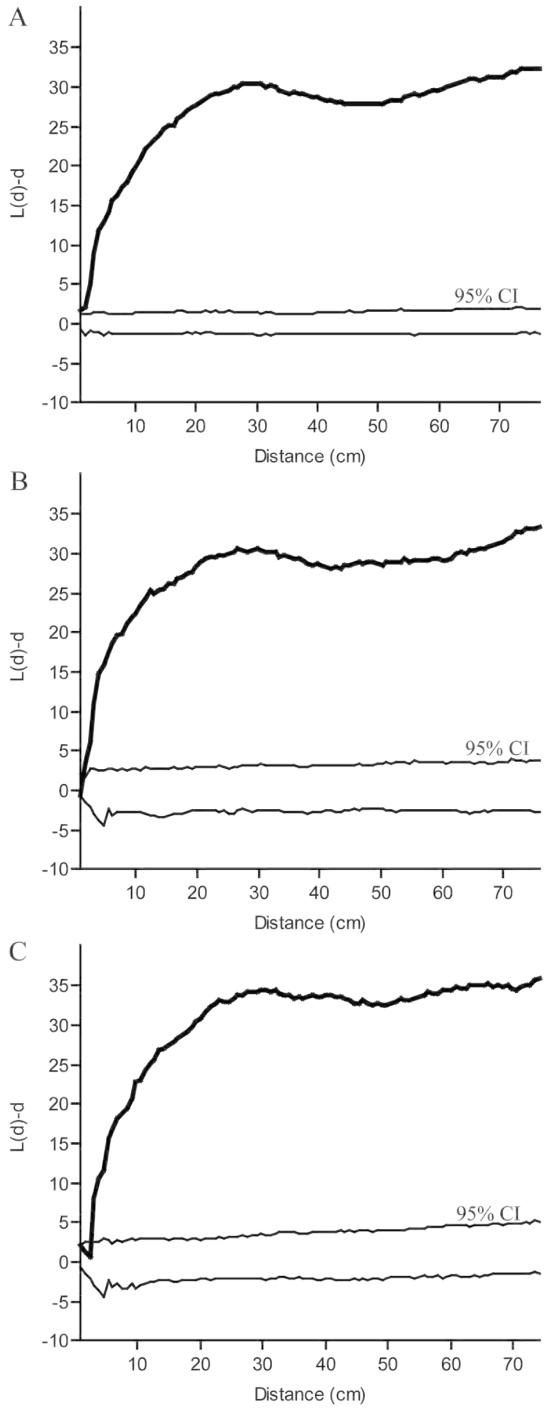

FIGURE II-10 – Ripley's K analysis, L(d)-d, of edrioasteroids on the Maysville hardground. All are above the 95% confidence level of complete spatial randomness (CSR), indicating clustering (but see C). A) All edrioasteroids. B) *Curvitriordo stecki*. C) *Carneyella ulrichi* is above the 95% confidence level except at very small (<2 cm) scales.

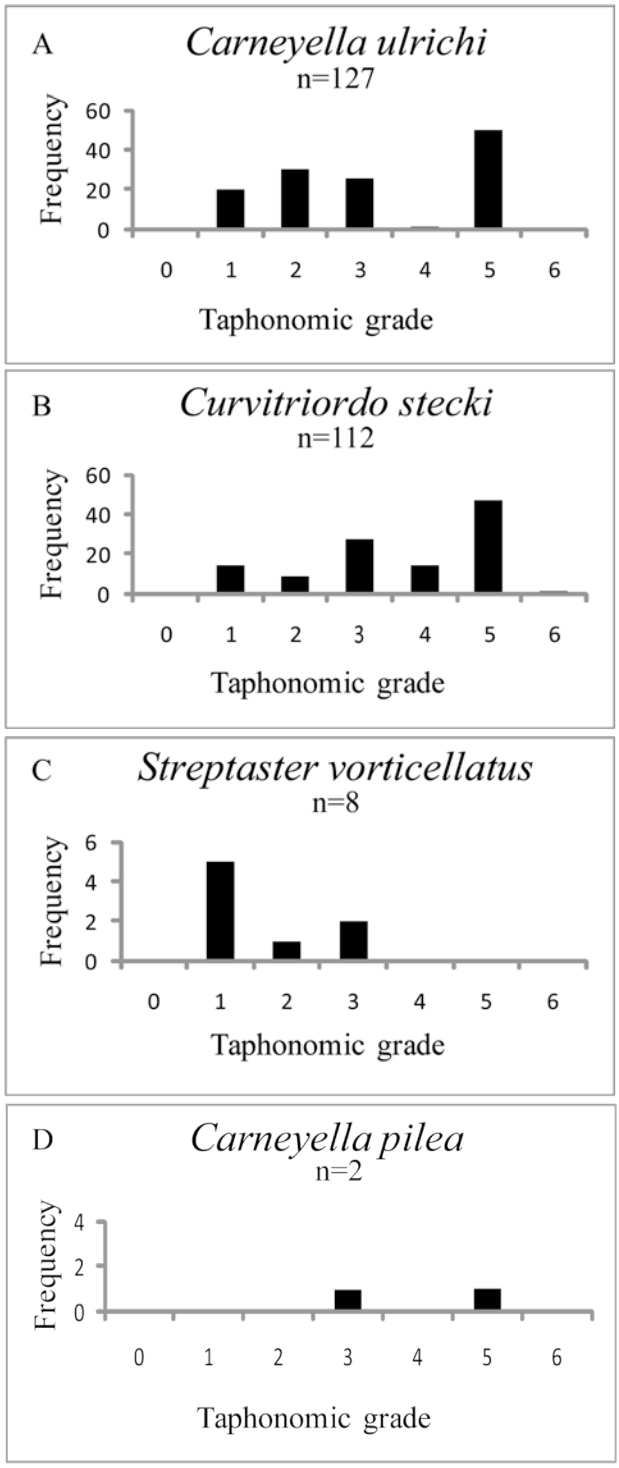

FIGURE II-11 – Histograms showing taphonomic grade of edrioasteroids. *Carneyella ulrichi* and *Curvitriordo* show taphonomic similarity. *Streptaster vorticellatus* shows low taphonomic grades indicating good preservation potential. See Table II-2 for further explanation.

III. A PALEOECOLOGIC COMPARISON OF TWO EDRIOASTEROID (ECHINODERMATA) ENCRUSTED PAVEMENTS FROM THE UPPER ORDOVICIAN CORRYVILLE FORMATION OF FLORENCE, KY AND THE MIAMITOWN SHALE OF SHARONVILLE, OH

This chapter is a reformatted version of a paper, by the same name, to be submitted to the journal PALAIOS by René A. Shroat-Lewis, Colin D. Sumrall, Michael L. McKinney, and David L. Meyer.

ABSTRACT

Occurrences of articulated multi-element skeletons of edrioasteroids provide evidence of sudden burial and an opportunity for detailed paleoecologic analysis. This study examines two catastrophically buried communities of edrioasteroids from Florence, Kentucky and Sharonville, Ohio. On these two pavements edrioasteroids *Isorophus cincinnatiensis*, *Streptaster vorticellatus*, and *Carneyella pilea* utilized brachiopod and mollusc shells as hard substrate for attachment. Age structure analysis for specimens of *Isorophus cincinnatiensis* on both pavements show right-skewed distributions attributed to high juvenile mortality. Thecae on the Florence pavement show slight bipolar preferential orientation, likely in response to current flow, whereas no preferential thecal orientation exists for specimens on the Sharonville pavement. Spatial analysis of the Florence pavement indicates a clustered edrioasteroid distribution due to multiple edrioasteroids attached to single brachiopod shells. Edrioasteroid margin deformation, in response to inter- and intraspecific competition, provides evidence that edrioasteroids were unable to move once attached to the substrate. Spatial analysis for *Isorophus cincinnatiensis* on the Sharonville pavement, however, shows few instances of multiple edrioasteroids attached to individual shells. Instead, this clustered distribution suggests enhanced encrustation in areas of enhanced feeding conditions or reproductive success. The high degree of thecal disarticulation suggests postmortem bloating and rupture.

INTRODUCTION AND PREVIOUS WORK

Paleoecology uses the fossil record to interpret and reconstruct life habits of past organisms and environments. By examining well-preserved fossil populations we can assess the relationship between organisms and their surrounding environment, the distribution of organisms within their environment, and the nature of their interactions (Kauffman and Scott, 1976). However, preservation of entire populations of organisms is rarely encountered in the fossil record because of an absence of preservable hard parts or rapid burial. Decomposition slows when obrution, or smothering of organisms by fine-grained sediment, occurs because the sediment cover holds organisms in place, removing the carcasses from the sediment/water interface and protecting them from further disruption by scavengers. Because of near instantaneous burial, such events also allow the examination of a census population, rather than time averaged faunas.

Although they have a rich fossil record, well-preserved echinoderm populations are rare because post-mortem disarticulation of their multi-element skeleton is rapid, occurring within one to two weeks under normal marine conditions (Meyer, 1971; Liddell, 1975; Kidwell and Baumiller, 1990; Greenstein, 1991; Donovan, 1991). Brett et al. (1997) explored echinoderm taphonomy in depth and assigned echinoderms to one of three categories based upon ease of skeletal disarticulation. Type I echinoderms have calcite plates held together by soft tissue and ligaments. Fully articulated specimens are rare in the fossil record because the soft tissue that holds plates together quickly decays, allowing disarticulation and scattering of the skeletal elements. Edrioasteroids, asteroids, and ophiuroids fall into this category. Type II echinoderms, which includes most species

of crinoids and most regular echinoids, have skeletal elements that are more tightly articulated than Type I echinoderms, and are therefore more likely to be preserved intact. Type III echinoderms, which include blastoids and some crinoids, have tightly articulated skeletons, and are thus commonly found in the fossil record.

In addition to being Type I (difficult to preserve) echinoderms, edrioasteroids, are also obligate-encrusting echinoderms. A wide range of potentially encrustable surfaces, such as carbonate hardgrounds, shell pavements, living shelled organisms, or cobbles occurred throughout the Paleozoic (Brett and Liddell, 1978; Waddington, 1980; Wilson, 1985; Meyer, 1990; Guensburg and Sprinkle, 1994; Sumrall, 2000; Sumrall and Zamora, 2011), but unless catastrophically buried, the presence of these Type I echinoderms cannot be recognized except by the presence of isolated edrioasteroid ossicles. Furthermore, when discovered, well-preserved pavements containing edrioasteroids are rarely collected in their entirety, thus precluding the study of distributional paleoecology of taxa in these ancient environments.

Shell beds are defined as relatively dense accumulations of skeletal material and sedimentary matrix (Kidwell et al., 1986). These concentrations are commonly composed of shells from brachiopods, bivalves, and gastropods, with other faunal elements including bryozoan remains and echinoderm debris (Li and Droser, 1999). The degree of preservation varies greatly from well-preserved intact shells to highly fragmented specimens and is dependent upon the skeletal type and depositional environment (Li and Droser, 1999). However, these shell beds often provide the only suitable substrate necessary for encrusting organisms.

Several obrution surfaces with populations of edrioasteroids have been reported from the Cincinnatian Series of Ohio and Kentucky (Kesling and Mintz, 1960; Meyer, 1990; Dattilo, 1998; Goad et al., 2006; Roberts et al., 2006; Dattilo et al., 2009; Sumrall, 2010; Shroat-Lewis et al., 2011). This project examines two edrioasteroid-encrusted shell pavements located within the Corryville Formation and Miamitown Shale (Fig. III-1). Suitable attachment substrate on these surfaces is relegated to isolated shells, effectively generating islands of attachment over a discontinuous surface. Consequently, they are fundamentally different from the hardground described by Shroat-Lewis et al., (2011) where edrioasteroids encrusted a more or less contiguous hard substrate.

The Florence pavement (Fig. III-2), was collected in 1977 from a construction site in Florence, Kentucky and is currently housed at the University of Cincinnati. Three common Cincinnatian edrioasteroid species encrust shells on the surface: *Isorophus cincinnatiensis* (Roemer, 1851), *Streptaster vorticellatus* (Hall, 1866), and *Carneyella pilea* (Hall, 1866). Edrioasteroids are found attached to shells of the brachiopod *Rafinesquina* (Hall and Clarke, 1892), which provided suitable substrate for attachment. Meyer (1990) first examined the Florence shell pavement, noting edrioasteroid population structure, substrate preference, location on host shell, and preservational style of the edrioasteroids. He made note of the tendency for juvenile edrioasteroids to attach close to the downward-facing shell margins of the brachiopods, which, he inferred, protected the edrioasteroid from direct sedimentation that may have clogged the respiratory and feeding surfaces.

The Sharonville pavement (Fig. III-3), is a mollusc-rich shell pavement from the Upper Ordovician Miamitown Shale studied *in situ* in an educational display at the Trammel Fossil Park in Sharonville, Ohio. Two species of edrioasteroids, *Isorophus cincinnatiensis* and *Carneyella pilea*, are found encrusting the common Ordovician bivalves *Ambonychia* (Hall, 1847) and *Modiolopsus* (Hall, 1847). Few examples of encrustation on *Rafinesquina* and *Hebertella* (Hall and Clarke, 1892) brachiopods, *Loxoplocus* (Fischer, 1885) gastropods, and bryozoans have been documented. The surface of the pavement is relatively flat with topographic highs of a few millimeters provided by the mollusc shells.

Our principle objective in this paper is to attempt a holistic reconstruction of these two edrioasteroid populations and their distributional ecology. We examined the population composition, orientation preference, spatial patterns, and taphonomy separately for each pavement, to test whether: 1) size frequency distributions will conform to an ideal distribution, with specimens of all ages represented; 2) edrioasteroids orient preferentially in response to paleocurrent flow; 3) edrioasteroids are clustered upon the pavement; and, 4) obrution preserved the edrioasteroids' delicate structures, minimizing the degree of disarticulation across the population.

THE FLORENCE PAVEMENT

Geologic Setting

The Florence pavement (Fig. III-2) was collected from a construction site located 150 m west of Mall Road and 200 m north of U.S. Route 42-127, Boone County, Kentucky (Meyer, 1990). The edrioasteroid bed was removed from strata equivalent to

the Corryville Member of the Grant Lake Formation as defined by Tobin (1986). The Corryville Member was deposited in an off-shelf environment, situated along a gently sloping carbonate ramp in a shallow empiric sea (Tobin, 1986). Episodic storm events, evidenced by storm beds and storm-related structures, occur frequently throughout the Corryville Member (Tobin, 1986).

The Corryville Member consisted of mud-rich packstone and wackestone interbedded with shale. It contains the most diverse open-marine fauna of any stratigraphic unit found in the Cincinnatian Series (Tobin, 1986; Goldman, 1998). Macroinvertebrate fauna is composed of a range of *Flexicalymene* and *Isotelus* (Dekay, 1824) trilobites, crinoid columnals, and ramose bryozoans (Goldman, 1998). Shell pavements occur at the upper surfaces of packstone intervals and contain whole and disarticulated *Rafinesquina* and *Zygospira* (Hall, 1862) brachiopods. Corryville fossils, although largely disarticulated, show little evidence of abrasion, suggesting only minor transportation (Meyer et al., 1981; Goldman, 1998). Although edrioasteroids are rare in the Corryville Member, two populations of well-preserved, articulated edrioasteroids occur attached to *Rafinesquina* brachiopod shell pavements (Meyer et al., 1981; Meyer, 1990; Dattilo et al., 2009).

Methods

The Florence brachiopod pavement was reassembled in sections at the University of Cincinnati in Cincinnati, OH. Six perimeter pieces and a small section in the interior of the pavement originally examined by Meyer (1990) were not located at the time of reconstruction. Individual maps of the pavement were made using plastic overlays. The

location of edrioasteroids, brachiopods and bivalves with encrusting edrioasteroids, all brachiopods, and all bivalves were mapped on each overlay. Brachiopod and bivalve shells less than 50 percent complete were not mapped on the overlays. Photographs of the plastic overlays were made and digitally stitched together using Adobe Photoshop to produce a map of the pavement in its entirety.

For each edrioasteroid, the species name, maximum theca diameter, orientation of the anterior-posterior axis in relationship to present day North, substrate type, X-Y position on a Euclidian grid, and taphonomic grade were recorded. Histograms of maximum edrioasteroid theca diameter were constructed to assess population structure. Thecal diameters for incomplete specimens were estimated by doubling the radius.

The orientation of the edrioasteroid A/P axis was determined by using either the inherent bilateral symmetry of the oral area, the ambulacral curvature asymmetry, or position of the anal pore (Shroat-Lewis et al., 2011). Azimuth of the edrioasteroid A ambulacrum was used to determine thecal orientation relative to true North. These data were arbitrarily binned in 30-degree increments and used to construct rose diagrams.

The Rayleigh Test for Randomness of Circular Data was used to determine strength of preferred orientation at the 95% significance level for each species. The vector mean direction is given by:

$$\bar{\Theta} = \frac{\sum \sin\Theta}{\sum \cos\Theta}$$

and the R value (Rayleigh's spread) or strength of resultant vector, is given by:

$$\bar{R} = \frac{\sqrt{\sum \sin\Theta^2 + \sum \cos\Theta^2}}{n}$$

where Θ = direction and *n* = number of individuals. $\overline{R}$ is tested against a random distribution using Rayleigh's test for directional data (Davis, 2002). An $\overline{R}$ value close to one indicates existence of a preferred orientation exists, whereas an $\overline{R}$ value close to zero indicates no preferred orientation. To test for bipolarity of these circular orientation data, we transformed the data by multiplying the angles by two. We then compute the vector mean direction and $\overline{R}$ value for the transformed data as above.

The choice of substrate attachment site was noted, and gives information about the degree of lithification of the seafloor at the time of edrioasteroid settlement. Edrioasteroid attachment location, i.e. margin, apex, umbo on brachiopods and bivalves was noted.

The distribution of organisms on the obrution surface is important as it give us clues to biotic relationships, reproduction strategies, and degree of lithification of the substrate. Spatial relationships examined on the Florence Pavement include: 1) edrioasteroids; 2) *Rafinesquina* brachiopods and bivalve shells with encrusting edrioasteroids; 3) all *Rafinesquina* brachiopods; and, 4) all bivalves. The center of each organism of interest was used to determine X-Y position on the pavement. Adobe Illustrator was used to determine area and perimeter of each pavement.

Nearest Neighbor Analysis (NNA) was performed using Paleontological Statistics (PAST) software, Version 2.08 (Hammer and Harper, 2006). This spatial analysis technique compares the observed distance between nearest individuals to the expected mean distance between randomly distributed individuals. The expected mean difference, with correction for map edge effects, is calculated as:

$$\overline{R} = 0.5\sqrt{\frac{A}{n}} + \left[0.051 + \left(\frac{0.412}{\sqrt{n}}\right)\right]\left(\frac{p}{n}\right)$$

where A = area of the map, n = number of individuals, and p = map perimeter (Davis, 2002). The ratio of these mean values (R) measures the departure from Complete Spatial Randomness (CSR). An R < 1 indicates clustering of the individuals, an R = 1 indicates a random distribution, while an R > 1 indicates dispersal of individuals. The Z statistic was calculated to determine if the observed pattern differs significantly from a random distribution. A Z-value of < -1.96 or > 1.96 indicates a 95% confidence that the individuals are not randomly distributed (Sumrall et al., 2009).

Taphonomic grade, an assessment of the degree of edrioasteroid thecal disarticulation (Table III-1), was determined for each edrioasteroid following the method of Shroat-Lewis et al. (2011). This method uses seven progressive grades of thecal disarticulation. Fully articulated, inflated specimens receive a taphonomic grade of zero. Taphonomic grade one is assigned to those edrioasteroids that are fully articulated, yet have become deflated in response to sediment overburden. Taphonomic grade two is characterized by disruption of the ambulacral plates, which remain at slightly higher relief than the interambulacral plates after post-mortem deflation of the theca. Shifting of the interambulacral plates places an edrioasteroid into taphonomic grade three. The edrioasteroid peripheral rim is more robust than the ambulacral and interambulacral plates, and therefore, the last feature of the edrioasteroid to disarticulate. In taphonomic grade four only the peripheral rim remains completely intact and there may be no coherence of plates, if present. Edrioasteroids with an incomplete peripheral rim are

assigned to taphonomic grade five. Bioturbation by worms or other burrowing organisms that disrupt the edrioasteroid theca receive a taphonomic grade of six.

Results for the Florence Pavement

The Florence brachiopod pavement (Fig. III-2) is relatively flat with only a few centimeters of relief. Topographic highs reflect occurrence of brachiopod shells. Of the 350 individual edrioasteroids originally noted by Meyer (1990), 322 could be located on the intact pavement for analysis. The echinoderm fauna includes three species of edrioasteroids: *Isorophus cincinnatiensis* (n = 295), *Streptaster vorticellatus* (n =21), and *Carneyella pilea* (n = 6). The 322 edrioasteroids are attached across a total surface area of 11.5 m^2, yielding a density of 28 edrioasteroids per square meter. When examined separately, specimens of *I. cincinnatiensis* had an overall density of 25.6 specimens per m^2, *S. vorticellatus* had an overall density of 1.8 specimens per m^2, and *C. pilea* had an overall density of 0.5 specimens per m^2. Other examined fauna includes 2,638 *Rafinesquina* brachiopods that have an overall density of 188.5 specimens per m^2, and 61 bivalves with an overall density of 5.3 specimens per m^2.

Two of the three species of edrioasteroids occurred in sufficient numbers for population structure analysis. Of the 21 specimens of *S. vorticellatus*, 13 could be measured for diameter (Fig. III-4A). Remaining samples were either partially buried or taphonomically disrupted. Size frequency analysis of thecal diameter shows a normal distribution with a mean diameter of 11.96 mm, standard deviation of 4.83 mm, median of 11.72 mm, minimum of 3.44 mm, maximum of 20.99 mm, and a skewness of 0.07. Caution should be used with analysis of *S. vorticellatus* because of the small population

size. Only six specimens of *C. pilea* were found on the hardground with thecal diameters ranging from 1.36 mm to 13.33 mm (Fig. III-4B). Of the 295 specimens of *I. cincinnatiensis*, 289 could be measured for diameter. Size frequency analysis of thecal diameter shows a right-skewed distribution (Fig. III-4C) with a mean diameter of 9.5 mm, standard deviation of 5.76 mm, mode of 8.0 mm, median of 7.99 mm, minimum of 1.56 mm, maximum of 34.05 mm, and skewness of 1.92.

Of the three species of edrioasteroids occurring on the Florence pavement, only *I. cincinnatiensis* occurs in sufficient numbers for orientation analysis. Of the 295 specimens, 167 could be measured for orientation of the A ambulacrum (Fig. III-5A). Vector analysis gives an azimuth of 294.52 degrees, an $\overline{R}$ value of 0.04, and a p-value of 0.76, indicating that no preferential unidirectional orientation exists. Data were then doubled and the test for bipolarity conducted. Vector analysis gives an azimuth of 43.05 degrees, an $\overline{R}$ value of 0.13, and a p-value of 0.054, indicating that orientation is preferential, yet barely significant. Both *S. vorticellatus* and *C. pilea* had too few specimens for meaningful analysis.

The distribution of edrioasteroids on different substrates is outlined in Table III-2. Of the 322 edrioasteroids, 309 are attached to the shells of brachiopods, with 220 specimens (68%) found attached near brachiopod shell margins. Those not found near the margin are attached closer to the apex of the shell with some edrioasteroids large enough to dominate the entire exposed shell surface.

Interspecific Nearest Neighbor Analysis (NNA) conducted for all specimens (Fig. III-6A) of edrioasteroids found on this surface reveal an observed mean distance of 5.44

cm, an expected mean distance of 9.62 cm, a distribution score of R = 0.57 and a Z statistic of -14.78 ($p < 0.001$), indicating a clustered distribution. Intraspecific Nearest Neighbor Analysis was conducted for two of the three species of edrioasteroids. Nearest Neighbor Analysis of the 295 *I. cincinnatiensis* specimens (Fig. III-6B) gave an observed mean distance of 5.61 cm, an expected mean distance of 10.44 cm, a distribution score of R = 0.54, and a Z statistic of -540.47 ($p < 0.001$), indicating a clustered distribution on the substrate. Nearest neighbor analysis for 21 specimens of *S. vorticellatus* (Fig. III-6C) gave an observed mean distance of 27.65 cm, an expected mean distance of 52.33 cm, a distribution score of R = 0.53, and a Z statistic of -106.14 ($p < 0.001$) indicating a clustered distribution on the substrate. *C. pilea* (n = 6) (Fig. III-6D) had too few specimens for meaningful analysis.

Nearest neighbor analysis for the 165 *Rafinesquina* brachiopods and bivalves with encrusting edrioasteroids (Fig. III-7A) gave an observed mean distance of 13.88 cm, an expected mean distance of 14.35 cm, a distribution score of R = 0.97, and a Z statistic of 1.07 ($p = 0.28$) indicating a random distribution on the substrate. Nearest neighbor analysis for the 2,638 *Rafinesquina* brachiopods (Fig. III-7B) gave an observed mean distance of 4.04 cm, an expected mean distance of 3.35 cm, a distribution score of R = 1.21, and a Z statistic of 1076.58 ($p < 0.001$) indicating a slightly dispersed distribution upon the substrate. Finally, nearest neighbor analysis of the 61 bivalves (Fig. III-7C) gave an observed mean distance of 15.22 cm, an expected mean distance of 25.58 cm, a distribution score of R = 0.59, and a Z statistic of -166.99 ($p < 0.01$) indicating a clustered distribution on the substrate.

Edrioasteroids were assessed for taphonomic grade using the parameters found in Table III-1. Of the 295 specimens of *I. cincinnatiensis*, 283 could be assessed for taphonomic grade. Partial sediment cover obscured the remaining specimens. Specimens of *I. cincinnatiensis* showed wide variation in taphonomic grade (Fig. III-8A) with the majority (n = 135) falling within taphonomic grade five. Of the 21 specimens of *S. vorticellatus*, 16 could be measured for taphonomic grade, with 14 specimens assigned to category five (Fig. III-8B). Of the six specimens of *C. pilea*, four specimens received a taphonomic score of five (Fig. III-8C).

Paleoecologic Interpretation

In Meyer's (1990) original study of the Florence pavement, 350 edrioasteroids were noted on the hardground with 68% of the population composed of *I. cincinnatiensis* (n = 238), 3% *S. vorticellatus* (n = 11), 8% *C. pilea* (n = 29), and 20.5% unidentified (n = 72). Meyer (1990) states the majority of unidentified specimens are likely *I. cincinnatiensis*, thereby making their overall proportion higher. When reexamined for this study, taxonomic identification of the 322 edrioasteroids show a very different population distribution, with 91.6% of the population composed of *I. cincinnatiensis* (n = 295), 6.5% *S. vorticellatus* (n = 21), and 1.9% *C. pilea* (n = 6). Although there is a deficit of 28 edrioasteroids in our study, we feel confident that our population composition is accurate as we were able to assign species identity to those previously unidentified (Meyer, 1990).

Overall density of 28 edrioasteroids per m^2 on the hardground compares to that seen on other edrioasteroid pavements (Sumrall 2010; Shroat-Lewis et al., 2011), but is

much lower than that seen on the most densely populated surfaces where densities reached a peak of 5,000 individuals per square meter (Sumrall et al., 2006; Sumrall et al., 2009). At the other extreme, edrioasteroid densities have been observed as low as 2 per square meter (Sumrall, 2001). The relatively low density of edrioasteroids on the Florence pavement likely results from: 1) competition for resources; 2) an unstable environment resulting in low survival; or 3) an r-strategy for survival.

Edrioasteroid theca diameter, used as a proxy for age, allows population structure analysis. We anticipated that the size frequency distribution would conform to an ideal distribution, with specimens of all ages represented. Of the three species of edrioasteroids on the Florence pavement, only *I. cincinnatiensis* occurs in sufficient numbers for meaningful analysis of population structure. Population structure analyses were inconclusive for both *S. vorticellatus* (Fig. III-4A), with 13 specimens, and *C. pilea* (Fig. III-4B), with 6 specimens, because of their small population sizes. The population of *I. cincinnatiensis* (Fig. III-4C) shows a strongly right-skewed distribution with a pronounced peak occurring at the 6-8 mm size. These juvenile specimens dominate the population with representatives of all ontogenetic stages found. The high number of juveniles and few mature specimens, coupled with evidence of frequent storms, suggests *I. cincinnatiensis* was an r-strategist. Further, the high frequency of juvenile edrioasteroids may suggest that this was the result of a single spatfall that occurred shortly before entombment.

Non-transformed data indicate that no unidirectional preferential thecal orientation exists for any of the species of edrioasteroids on the Florence pavement (Fig.

III-5A). However, the test for bipolarity indicates that specimens of *I. cincinnatiensis* show weak preferential orientation upon the substrate (Fig. III-5B). Previous studies of edrioasteroid ambulacral orientation have found various results from no preferential orientation (Sumrall, 2001; Cornell et al., 2003; Sumrall, 2010; Shroat-Lewis et al., 2011), to weak (Roberts et al., 2006; Sumrall et al., 2009), to strongly preferred thecal orientation (Smith, 1983). We suggest that this weakly preferential ambulacral direction may have been in response to current direction, which may have provided the edrioasteroids with enhanced feeding opportunity. Both *S. vorticellatus* and *C. pilea*, with one and five specimens with measured orientations respectively, had too few specimens for meaningful analysis.

Spatial relationship examined on the Florence Pavement include: 1) edrioasteroids; 2) *Rafinesquina* brachiopods and bivalve shells with encrusting edrioasteroids; 3) all *Rafinesquina* brachiopods; and, 4) all bivalves. All analyses show clustering on the substrate except for the *Rafinesquina* brachiopods and bivalve shells with encrusting edrioasteroids. That the edrioasteroids are clustered on the surface as a whole, but shells they attach to are randomly distributed, suggest an underlying pattern to their distribution.

Specimens of *I. cincinnatiensis* are clustered as a result of frequent instances of multiple encrusters on a single shell rather than being spread out among unoccupied shells. Of the 165 encrusted shells, 55% are encrusted by one edrioasteroid, 44% are encrusted by 2-5 edrioasteroids, and 2% are encrusted by 6-10 edrioasteroids. These clustered distributions however may result from other factors, such as rapid, opportunistic

encrustation on shells after larval fertilization. Edrioasteroids that attached to non-ideal surfaces, such as the muddy seafloor, may not have survived.

Additionally, clustered spatial distributions are an effective method for improving reproductive success for sessile r-strategist organisms. With the release of gametes into the open water, fertilization success is dependent upon organism proximity. Since the goal of the r-strategist is to produce as many individuals as possible in a short time, dispersed populations would suffer from a reduction in population density if fertilization did not occur, which would then have a dramatic impact on future reproductive output and success (Levitan et al., 2002).

Third, right skewed distributions suggest low population survivorship. Clustering may therefore be a sign of shells where recruited individuals survived, whilst non-encrusted shells may reflect instances where juvenile recruits did not survive. As discussed later in this study, unusual bryozoan circular growth patterns can be seen (Fig. III-9A) on shell surfaces. We suggest the bryozoans mark the location of edrioasteroids that encrusted the shell, but perished prior to entombment. Further, other members of the edrioasteroid population may have settled in inappropriate areas, resulting in death for those individuals.

Finally, encrusted shells may have been located in areas of enhanced feeding opportunity. It may be that clusters of individuals are found where subtle differences in current across the substrate made these encrusted areas beneficial for food capture. This may be supported by the weak preferred orientation seen in the thecae of *I.*

cincinnatiensis. Therefore, the dispersal pattern may reflect those edrioasteroids that encrusted in areas where resources promoted survival.

We expect to see a clustering pattern when multiple individuals of *I. cincinnatiensis* are attached to individual brachiopod and bivalve shells. *Streptaster vorticellatus*, with 20 specimens attached to brachiopod and bivalve shells, were found clustered upon the substrate. Although interpretation with so few individuals is tenuous, we suggest the clustering pattern is the result of settlement in an area with preferred conditions, such as enhanced feeding opportunity or enhanced reproductive success. However, caution should be used with these results because of the small population size. Specimens of *C. pilea* had too few specimens for meaningful analysis.

With multiple encrusters vying for attachment space, instances of examples of inter- and intraspecific competition are likely to occur (Fig. III-9A-D). In Figure III-9A the relatively large trepostome bryozoan, found near the center of the hinge line, likely grew radially until it came into contact with the edrioasteroid. A 1 mm gap separates the bryozoan and edrioasteroid. No deformation of the edrioasteroid theca occurs. Sprinkle and Rodgers (2010) examined a similar instance of competition between an edrioasteroid and bryozoan. They suggest the edrioasteroid used its tube feet to suppress the growth of the bryozoan, keeping it as far away as possible from the ambulacra. Cyclostome bryozoans can also be seen encrusting the brachiopod in Figure III-9A. Close examination shows that these bryozoans generally grow in straight lines on this brachiopod shell. However, several instances of bryozoan circular growth patterns can be seen (Fig. III-9A). We suggest that this unusual pattern is the result of bryozoan growth

around the peripheral rim of small encrusting edrioasteroids. Death of the edrioasteroid would cause post-mortem disarticulation of the theca, leaving behind the empty bryozoan ring.

Other examples of interspecific competition can be seen in Figure III-9B where the specimen of *I. cincinnatiensis* is found overgrowing the base of the bryozoan. We suggest that the bryozoan was either unable to fend off the edrioasteroid or was dead prior to overtopping by the edrioasteroid. Figure III-9C highlights several instances of edrioasteroid margin deformation occurring where the edrioasteroids abut the bryozoans. There is no way to determine if the bryozoans are older or coeval with the edrioasteroids. However, we propose that the presence of a 1 mm separation between the edrioasteroid and bryozoan suggests that the bryozoan was likely alive at the time of contact with the edrioasteroid suppressing its growth in the area of contact, thereby deforming the peripheral rim. On this same shell, another edrioasteroid comes into contact with two bryozoans. Notice, however, that there is little to no separating space between the edrioasteroid and bryozoans. We suggest that in cases such as this, the bryozoans were either not alive or were unable to defend themselves as the edrioasteroid overtopped the bryozoan.

Instances of edrioasteroid intraspecific competition occur on this substrate as well (Fig. III-9D). The normal circular shape of the juvenile edrioasteroid theca has been flattened where it abuts the mature specimen. The peripheral rim plates of the mature specimen face upward at a steep angle where contact is made.

Of the 322 edrioasteroid specimens on the Florence pavement, 98% are found attached to 165 brachiopod and bivalve individuals. Meyer (1990) noted the tendency for small edrioasteroids to attach to the brachiopod and bivalve shells near the shell margins. Our results confirm those of Meyer (1990) with 69% of the edrioasteroids examined in this study found attached near the shell margin. Meyer (1990) suggested two hypotheses for this tendency – that the edrioasteroids benefited from the feeding currents of the brachiopods, and that the downfacing attachment site protected the edrioasteroids from sedimentation. Dattillo et al. (2009) investigated a different brachiopod pavement collected from the Florence area, finding many of the brachiopods had sediment-clearing moats that were considered to be the result of rapid snapping of the brachiopod valves, which cleared sediment from around the shell margins. Although this behavior would benefit encrusting edrioasteroid by keeping the loose, fine sediment away from the respiratory structures, we argue that this rapid snapping would cause backward movement of the brachiopod, much like the snapping of a scallop, leaving trace marks of this movement in the soft sediment. Instead, we argue that the brachiopods were not alive at the time of encrustation and that the moats are the result of overturned brachiopods resting on the seafloor in the more stable pedicle down position. As such, current flow over the convex-up valve position would scour the loose sediment around the shell margin via Bernoulli's principle and sediment plucking.

As a consequence of nearly instantaneous burial, we would predict that the degree of post-mortem disarticulation would be equal for all specimens of edrioasteroids found on the substrate. When edrioasteroids were assessed for taphonomic grade using the

parameters outlined in Table III-1, none were assigned a grade of zero. Specimens of *I. cincinnatiensis* (Fig. III-8A) show a wide range of taphonomic grades with the majority falling within taphonomic grades one and five. The majority of specimens of *S. vorticellatus*, with 87.5% (Fig. III-8B) and *C. pilea*, with 66.7% (Fig. III-8C) fall within taphonomic grade five. The presence of fully articulated specimens suggests that the edrioasteroids were buried rapidly by an obrution event. The variable taphonomic grades suggest that the initial influx of sediment was enough to kill the edrioasteroids by suffocation. Postmortem decay of the thecal connective tissue caused bloating and rupture, thereby causing disarticulation of the thecal plates.

THE SHARONVILLE PAVEMENT

Geologic Setting

The examined portion of the Sharonville pavement (Fig. III-3) is located *in situ* in an educational display at the Trammel Fossil Park in Sharonville, OH (39° 17'48.07" N, 84° 24'19.53" W). A smaller intact section has been reposited at the Frederick and Amey Geier Collections and Research Center of the Cincinnati Museum Center in Cincinnati, Ohio.

The Sharonville pavement is stratigraphically located within the Miamitown Shale, a mollusc-dominated unit consisting of interbedded thin- to medium-bedded limestone and shale, that occurs within the Great Lake Formation. Fluctuations in sea level likely account for the intertonguing facies with the limestone-rich intervals deposited during episodes of shallower water and shale-rich intervals deposited during episodes of deeper water (Dattilo, 1998).

The beds have a rich faunal composition (Fig. III-10A). Previous work by Goad et al. (2006) detailed the fauna, including: one species of cephalopod (Fig. III-10B), the brachiopods *Dalmanella* (Hall and Clarke, 1892), *Hebertella*, *Rafinesquina*, and *Zygospira*, the bivalves *Ambonychia* and *Modiolopsus*, the gastropods *Loxoplocus* and *Cyrtolites* (Conrad, 1838), *Cornulites* (Schlotheim, 1820) worm tubes, *Flexicalymene* (Shirley, 1936) trilobites, and three species of bryozoans. *Zygospira* brachiopods are commonly found in clusters on the surface in life position (Fig. III-10C) and encrusted by *Cornulites* worm tubes with their aperture oriented along the brachiopod commissure. Specimens of edrioasteroids *Isorophus cincinnatiensis* and *Carneyella pilea* are found encrusting the bivalves *Ambonychia* (Figs. III-10D and III-10E) and *Modiolopsus* (Fig. III-10D), brachiopods, gastropods, and bryozoans. Bryozoan encrustation of both internal and external surfaces of bivalve shells has been observed (Fig. III-10F) and demonstrates that the bivalves were not alive at the time of burial (Goad et al., 2006).

Methods

A single map of the Sharonville pavement was prepared using a clear plastic overlay. As with the Florence pavement, each edrioasteroid found on the examined surface received a unique designation and the following data were recorded: species name, maximum theca diameter, orientation of edrioasteroid A ambulacrum in relationship to present day North, substrate type, X-Y position on a Euclidian grid, and taphonomic grade.

Histograms of maximum edrioasteroid theca diameter were made and descriptive statistics were calculated. The orientation of edrioasteroids was determined following the

same protocol as for the Florence pavement. In cases where encrusting edrioasteroids were attached to either *Ambonicia* and *Modiolopsus* clam shells or *Rafinesquina* brachiopods, the orientation of the host was determined using the umbo as the rear of the shell. When attached to a gastropod, the gastropod aperture was designated as the rear for orientation purposes.

Spatial analysis software and techniques remained the same for analysis of the edrioasteroids found on the Sharonville pavement. Further, the spatial relationship of bivalves with encrusting edrioasteroids was examined. Finally, the technique for taphonomic analysis of the edrioasteroids remained the same as on the Florence pavement.

Results for the Sharonville Pavement

The Sharonville pavement includes 82 specimens of the edrioasteroid *I. cincinnatiensis* attached across a total surface area of 7.8 m^2, yielding an overall density of 10.5 edrioasteroids per m^2, approximately the same as the Florence pavement. No specimens of *C. pilea* were noted on the observed surface but are found elsewhere along the same horizon adjacent to the studied area. *Streptaster vorticellatus* has not been noted on this surface.

Of the 82 specimens of *I. cincinnatiensis*, 80 could be measured for thecal diameter. A histogram of the edrioasteroid population (Fig. III-11) shows considerable size variation with individuals ranging from 2.34 mm to 23.56 mm. Size frequency analysis of thecal diameter shows a slightly right-skewed distribution with a mean

diameter of 11.13 mm, standard deviation of 5.21 mm, median of 10.3 mm, and a skewness of 0.46.

Twenty-nine individuals could be measured for orientation of the A ambulacrum with the remainder being too taphonomically disrupted for orientation to be determined. Vector analysis gives an azimuth of 180.28 degrees (Fig. III-12A), an $\overline{R}$ value of 0.10, and a p-value of 0.74, indicating that no preferential direction exists. Using transformed orientation data for the bipolarity test, vector analysis gives a azimuth of 171.35 degrees, an $\overline{R}$ value of 0.12, and a p-value of 0.63, indicating that no preferred orientation exists.

Twenty-nine specimens of *I. cincinnatiensis* were found attached to *Ambonychia* bivalves, 18 on *Modiolopsus* bivalves, 12 on *Loxoplocus* gastropods, six on *Rafinesquina* brachiopods, four on *Hebertella* brachiopods, three on bryozoans, nine on sediment, and one on an unknown substrate (Table III-2). *Ambonychia* bivalves with encrusting edrioasteroids were examined for preferred orientation on the substrate. Vector analysis of the bivalves gives an azimuth of 157.15 degrees (Fig. III-12B), an $\overline{R}$ value of 0.15, and a p-value of 0.51. Both *Modiolopsus* bivalves and *Loxoplocus* gastropods with encrusting edrioasteroids had too few specimens for meaningful orientation analysis.

Intraspecific Nearest Neighbor Analysis was conducted for *I. cincinnatiensis*. Nearest Neighbor Analysis gave an observed mean distance of 11.71 cm, an expected mean distance of 16.34 cm, a distribution score of R = 0.72, and a Z statistic of -4.90 ($p < 0.001$), indicating a clustered distribution on the substrate (Fig. III-3). Bivalves on the substrate appear to be visually random though not measured for this study.

Edrioasteroid taphonomic grade was determined using the parameters found in Table III-1. Specimens of *Isorophus cincinnatiensis* showed little variation in taphonomic grade with the majority (n = 70) falling within taphonomic grade five (Fig. III-13).

Paleoecologic Interpretation

Edrioasteroids reach their peak of diversity during the Ordovician (Guensburg and Sprinkle, 2001; Shroat-Lewis and Sumrall, 2010), allowing for multispeciate, dense accumulations (Bell, 1975; Bell et al., 1976; Brett and Liddell, 1978; Waddington, 1980; Meyer, 1990; Sumrall 2010; Shroat-Lewis et al., 2011). On the Sharonville pavement however, both edrioasteroid diversity, with only *I. cincinnatiensis* represented on the study surface, and the overall density of 10.5 edrioasteroids per m^2 is low. Ninety percent of the edrioasteroids are found encrusting the bivalves *Ambonychia* and *Modiolopsus*, the gastropod *Loxoplocus*, the brachiopods *Hebertella* and *Rafinesquina*, and bryozoans. These hosts provided small-scale topographic highs for encrustation and were used to elevate the edrioasteroids off of the muddy seafloor.

The Sharonville mollusc pavement is a census assemblage of organisms alive at the time of rapid burial by obrution. The right-skewed size frequency distribution (Fig. III-11), with a higher proportion of juvenile-sized edrioasteroids to mature specimens, has been seen in other studies (Kammer et al., 1987; Meyer, 1990). As mentioned earlier in this study, the right skewed distribution is likely the result of r-selection. Positive skewness for specimens of *I. cincinnatiensis* on the Sharonville pavement is not as strong as for the same species on the Florence pavement. Earlier we suggested that the high

number of juveniles in the Florence population were likely the result of a recent spatfall. The paucity of juvenile *I. cincinnatiensis* specimens on the Sharonville pavement suggest a more mature population, with some juvenile specimens having already perished as a result of r-selection.

As with the edrioasteroids on the Florence pavement, specimens of *Isorophus cincinnatiensis* on the Sharonville pavement show no preferred thecal orientation (Fig. III-12A). Furthermore, no preferred orientation exists for the brachiopod *Ambonychia* (Fig. III-12B) that hosted encrusting edrioasteroids. Tests for bipolarity show lack of preferential orientation for both edrioasteroids and *Ambonychia*.

Nearest Neighbor Analysis shows that specimens of *I. cincinnatiensis* are clustered upon the shell pavement (Fig. III-3). Four instances of edrioasteroids encrusting the same shell are found on this surface. However, no interactions, such as margin deformation, are noted between edrioasteroids, suggesting that some other physical factor controlled the distribution of specimens on the substrate. Closer examination of the locations where edrioasteroids encrusted this (Fig. III-3) shows a North-South trend and may indicate direction of current flow. Clustering in this area in response to increased food availability supplied by the moving current likely occurred.

Eighty-five percent of the edrioasteroids found on the Sharonville pavement fall within taphonomic grade five (Fig. III-13). Goad et al., (2006) contend that a thick layer of sediment covered this surface, permanently burying the edrioasteroids. Therefore, the high grade of thecal disarticulation is likely the result of post-mortem decay and rotting of the connective tissue, which caused bloating and disruption of the thecal skeleton.

This mode of post-mortem disarticulation has been suggested by other studies (Cornell et al., 2003; Sumrall et al., 2006) and explains the wide range of taphonomic grades seen in this study.

Zygospira brachiopods found on the surface in life position (beak down) provide further evidence for rapid burial by a thick mud layer and suggest that the brachiopods were alive at the time of entombment. *Cornulites* worm tubes are found epibiotically attached to *Zygospira* brachiopods (Fig. III-10B). The cornulitid tube apertures are positioned so that the organisms were able to benefit from the brachiopod inhalent and exhalent feeding currents.

PALEOECOLOGIC COMPARISON

The catastrophic burial of these two shell pavements provides an opportunity for paleoecologic examination and comparison of two census assemblages that come from similar paleoenvironments and are nearly coeval, thereby holding both ecology and time constant.

Examination of both the Florence and Sharonville shell pavements show similar edrioasteroid faunal components, with populations of the edrioasteroids *I. cincinnatiensis*, *C. pilea*, and *S. vorticellatus* found on the Florence pavement and *I. cincinnatiensis* found on the Sharonville pavement. Although none were noted in our examination of the Sharonville pavement, specimens of *C. pilea* have been reported on the same stratigraphic horizon and no specimens of *S. vorticellatus* are known (Goad et al., 2006). Regardless, specimens of *C. pilea* make up a very small portion of edrioasteroids at both localities.

Our results show the edrioasteroid *I. cincinnatiensis* dominates both pavements. Edrioasteroid density distribution is also similar on both pavements. These findings are analogous to previous studies by Sumrall (2010) and Shroat-Lewis et al. (2011) of an edrioasteroid encrusted hardground from Maysville, Kentucky, with an edrioasteroid density population of 24 edrioasteroids per m^2. There, *Curvitriordo stecki* (closely related to *I. cincinnatiensis*) and *Carneyella ulrichi* (a close relative of *C. pilea*) dominate, comprising 47% and 48.6% percent of edrioasteroids whereas *Streptaster vorticellatus* and *Carneyella pilea* make up 3.5% and 0.9% percent respectively. The faunal similarities allow comparison between shell pavements and hardgrounds from similar Late Ordovician environments.

Size frequency distribution can provide valuable information about recruitment, growth, and mortality. Edrioasteroids on both shell pavements are right-skewed for populations of *I. cincinnatiensis*. These right-skewed distributions show a high number of juvenile individuals and fewer mature specimens. Such low survivorship suggest that in this environment, *I. cincinnatiensis* acted as an r-strategist, living in an unstable environment and producing many offspring that did not live to maturity. By comparison, edrioasteroid populations on the Maysville hardground examined by Sumrall (2010) and Shroat-Lewis et al. (2011) show size frequency distributions for the edrioasteroid *Carneyella ulrichi* to be strongly left-skewed, suggesting low juvenile mortality rate or decreased growth rate as individuals reached maturity. Size frequency distributions of specimens of *Curvitriordo stecki* showed a bimodal distribution, suggesting a hiatus in recruitment. The main mode of this distribution was also strongly left skewed suggesting

similar reproductive strategy as *Carneyella ulrichi*, but very different from that of *I. cincinnatiensis*.

Streptaster vorticellatus showed different patterns on the Florence pavement and Maysville hardground as well. On the Florence pavement, *Streptaster* showed a wide range in sizes ranging from 3.44 - 20.99 mm, with an average size of 11.96 mm and a standard deviation of 4.83 mm. *Streptaster* on the Maysville hardground had a tight unimodal distribution with specimens ranging from 19.4 - 24.36 mm in diameter, with an average size of 21.26 mm and a standard deviation of 1.72 mm.

Although both the Florence and Sharonville edrioasteroid populations are similar, when compared with edrioasteroids found on the Maysville hardground, we see very different histogram results. We suggest that the structural and behavioral differences between the species resulted from adaptations to living together in the same area. Harper et al. (1961) suggest three prerequisites for the successful occurrence of closely related species living in the same area: 1) must have different breeding behavior for each species so that the interspecific differences remain distinct; 2) must be able to tolerate the hazards which occur in the area they live; and 3) must differ enough so that they do not enter into a struggle for existence in which one succeeds at the expense of the other. The histograms of edrioasteroids examined on the Florence, Sharonville, and Maysville pavements reflect different population structures, suggesting different breeding seasons and survival ability in an environment with frequent storm activity.

The three pavements have specimens of the genus *Carneyella* encrusting the surface, yet the edrioasteroids differ strongly in their modal abundance. On the

Maysville hardground, *Carneyella ulrichi* is abundant with 12.1 specimens/m^2. However, *Carneyella* is infrequently found on the Florence pavement with 0.5 specimens/m^2, and is present, but not observed in this study of the Sharonville pavement. Shroat-Lewis et al. (2011) suggested edrioasteroid ambulacral width might be directly linked to resource partitioning. Specimens of *Carneyella* and *Isorophus* on the Florence pavement would be in direct competition for resources because both species have approximately the same ambulacral width. *Isorophus* outnumbers *Carneyella* by a 49:1 ratio on the Florence pavement. We suggest that the frequency of *Isorophus* on the substrate gave them an advantage over *Carneyella* when it came to catching food particles in the current.

Further, as mentioned previously, differences in the population structure of *Streptaster vorticellatus* between the Maysville hardground and Florence pavement may give us insight into the age/size at which this species reaches reproductive maturity. If the specimens of *S. vorticellatus* on both pavements were sexually mature then the lack of juveniles on the Maysville hardground may suggest that none survived the latest breeding season, or that the two specimens were of the same sex and unable to reproduce.

Although it seems reasonable to assume that sessile organisms such as edrioasteroids would orient preferentially in response to current flow this pattern is weak to non-existant in Ordovician edrioasteroid of the Cincinnati region. However, a weak bipolar preferential orientation pattern emerges when specimens of *I. cincinnatiensis* on the Florence pavement (Fig. III-5B) were examined. We suggest that this bipolar trend

may indicate a preference to the prevailing current, aligning the edrioasteroids so that feeding opportunity was enhanced and fouling of the oral area did not occur.

Nearest Neighbor Analysis on the Florence pavement (Fig. III-6B) and the Sharonville pavement (Fig. III-3) show specimens of *I. cincinnatiensis* are clustered upon the hardground. We propose the following explanations for the clustered pattern exhibited by these sessile organisms. On the Florence pavement, the brachiopod and mollusc shells sat upon a muddy seafloor. Since edrioasteroids require a firm substrate for attachment it is doubtful that they would attach directly to the muddy substrate located between the brachiopod and mollusc shells. Instead, the edrioasteroids attached to the shells, with instances of multiple edrioasteroids encrusting a single brachiopod shell occurring. This is much different than the encrusting pattern found on the Maysville hardground (Sumrall, 2010; Shroat-Lewis et al., 2011) since much of that carbonate hardground was available for encrustation.

Although the edrioasteroids found on the Sharonville pavement are also attached to shells, we do not see the same settlement pattern for specimens of *I. cincinnatiensis*. Only four instances of more than one edrioasteroid attached to a bivalve or gastropod shell were noted. Therefore, we must consider alternative hypotheses to explain the clustering pattern. First, we suggest that the edrioasteroids may have been clustered in an area with a steady current that provided increased feeding opportunity. As sessile, encrusting organisms, edrioasteroids rely upon the movement of water, which carries food particles, for feeding success. Studies by Levitan et al. (1992) show that rapid dilution of gametes causes the success of fertilization to be proximity dependent.

Therefore, it would be important for these sessile organisms to be close in order to maximize the success of fertilization. Other suggestions for the clustering behavior of edrioasteroids include larval transportation as a population by currents and influence by adults who had some success where they settled.

Multiple instances of inter- and intraspecific interactions, such as margin deformation, are noted between edrioasteroids and bryozoans on the Florence pavement (Fig. III-9A-D). Two different patterns are noted with occurrences of edrioasteroid and bryozoan interactions. In some cases a <1 mm gap exists between the two faunal elements (Fig. III-9A), whereas other occurrences show the edrioasteroid overgrowing the bryozoan (Fig. III-9B). Although we cannot be certain if the bryozoans were alive at the time of interaction, we suggest that the presence of a gap indicates that both faunal elements were alive. The bryozoans may have used body extensions, which provided defensive and offensive mechanisms to prevent inter- and intraspecific faunal overgrowth. We cannot determine if the absence of a gap indicates that one of the faunal elements was dead as instances of overgrowth where both faunal elements were alive has been previously documented (Sprinkle and Rodgers, 2010). Our findings, coupled with the presence of interspecific interactions resulting in margin deformation of both edrioasteroids, agrees with the findings of Sumrall and Sprinkle (1992) who argued that once attached, edrioasteroids did not have the ability to move to avoid such interactions.

All species of edrioasteroids on both shell pavements received high taphonomic grades. On the Florence pavement, 47.7% of specimens of *I. cincinnatiensis* (Fig. III-8A), 87.5% of specimens of *S. vorticellatus* (Fig. III-8B), and 67% of specimens of *C.*

pilea (Fig. III-8C) fell within taphonomic grade five. On the Sharonville pavement, 85% of the specimens of *I. cincinnatiensis* (Fig. III-13) fell within taphonomic grade five. The influx of a thick layer of siliciclastic mud smothered the edrioasteroids, killing them nearly instantaneously and preserving them whole. However, postmortem bloat and rupture, as a result of decay of the connective tissue, is likely responsible for the high degree of edrioasteroid disarticulation.

SUMMARY

In depth examination of the two Ordovician hard substrates lead to the following conclusions:

1. Population structure for populations of *I. cincinnatiensis* on both the Florence and Sharonville pavements were right-skewed with more juveniles than adults.
2. Tests for bipolarity on the Florence pavement show specimens of *I. cincinnatiensis* are weakly preferentially oriented on the substrate.
3. Edrioasteroids exhibited no preferential orientation on the Sharonville pavement.
4. Brachiopods and molluscs on the examined pavements provided the necessary hard substrate for edrioasteroid encrustation.
5. Multiple edrioasteroid individuals attached to a brachiopod shell enhance the clustering pattern.
6. Specimens of *I. cincinnatiensis* are clustered on the Sharonville pavement though not because of numerous individuals per shell.

7. Edrioasteroid marginal deformation and bryozoan overgrowth suggests edrioasteroids were incapable of movement once attached to the substrate.
8. High taphonomic grade found on the Florence and Sharonville pavements suggests post-mortem thecal bloat and rupture.

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APPENDIX III

TABLE III-1 – Taphonomic grading scale describes degree of disarticulation (From Shroat-Lewis et al., 2011).

Grade	Appearance of edrioasteroid theca
0	Fully articulated and complete. Theca inflated.
1	Thecal collapse. All plates and ambulacra intact.
2	Cover plates begin to disarticulate. Shifted disruptions of theca.
3	Interambulacral plates begin to shift.
4	Only peripheral ring remains intact. No coherence with plates, if present.
5	Peripheral ring is incomplete.
6	Bioturbation disturbance present (i.e., worm burrows).

TABLE III-2 – List of organisms and substrate preferences for the Florence and Sharonville pavements.

	Substrate	Raf	Heb	Zyg	Amb	Mod	Gas	Bry	Deb	Sed	Unk
	Species										
Florence	*Isorophus cincinnatiensis*	285	0	0	0	0	0	0	3	5	2
	Streptaster vorticellatus	18	0	0	0	0	0	0	1	2	0
	Carneyella pilea	6	0	0	0	0	0	0	0	0	0
	Total										
Sharonville	*Isorophus cincinnatiensis*	6	4	0	29	18	12	3	1	9	0

Raf = *Rafinesquina*, Heb = *Hebertella*, Zyg = *Zygospira*, Amb = *Ambonichia*, Mod = *Modiolopsus*, Gas = gastropod, Bry = bryozoan, Deb = debris, Sed = sediment, Unk = unknown

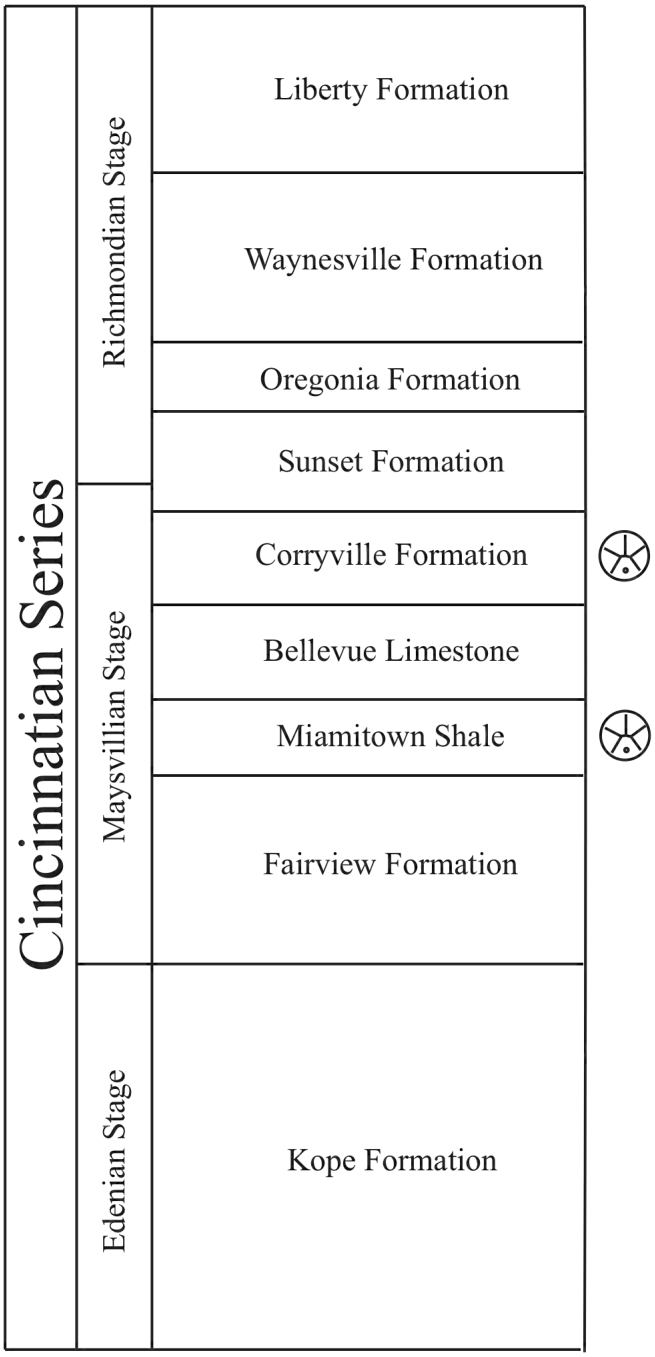

FIGURE III-1 – Stratigraphic column of the Cincinnatian Series (modified from Meyer, 1990). Symbols indicate stratigraphic location of examined pavements. Not to scale vertically.

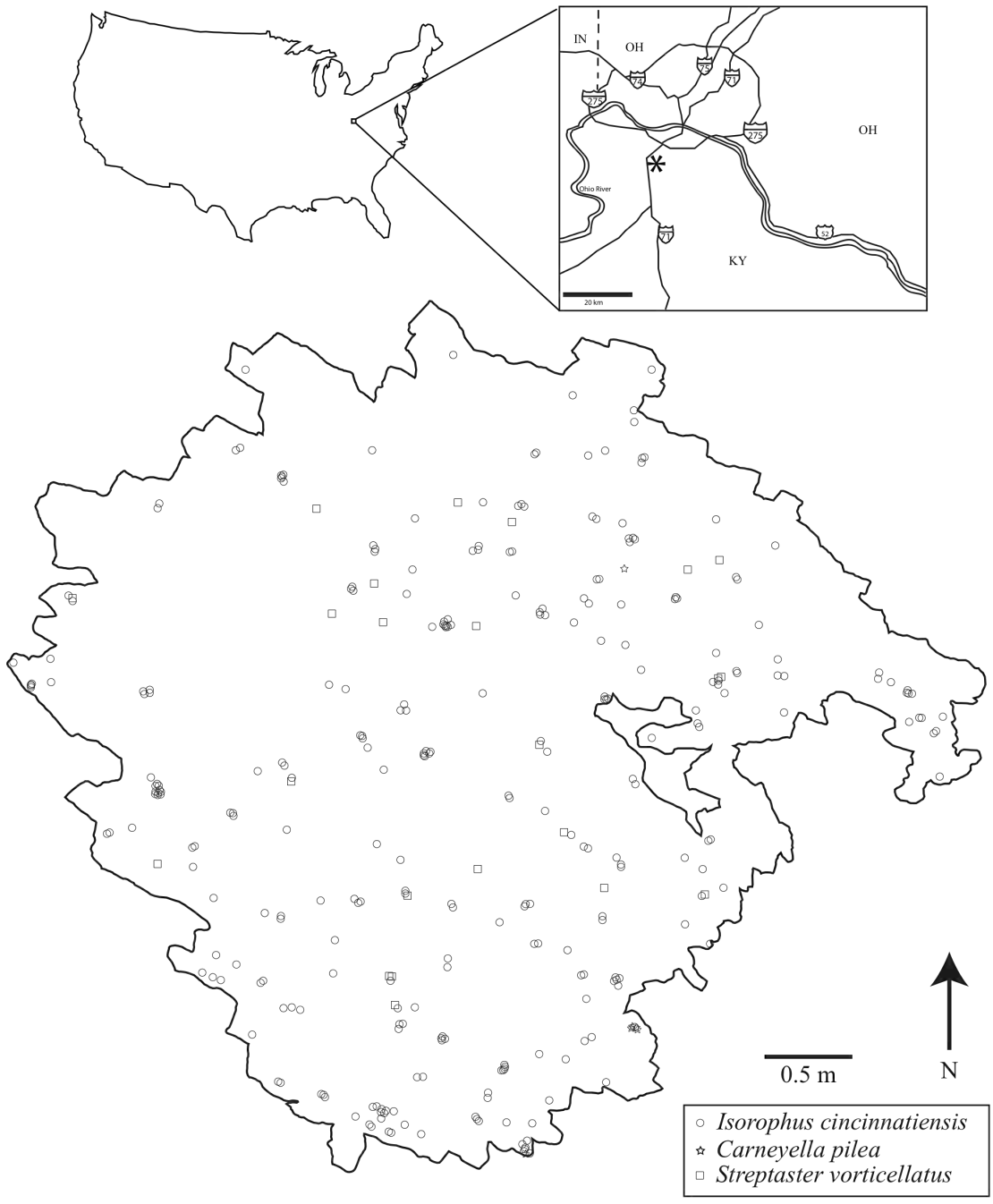

FIGURE III-2 – Map showing locations of edrioasteroids on the Florence brachiopod pavement. Asterisk on map insert shows location where pavement was collected.

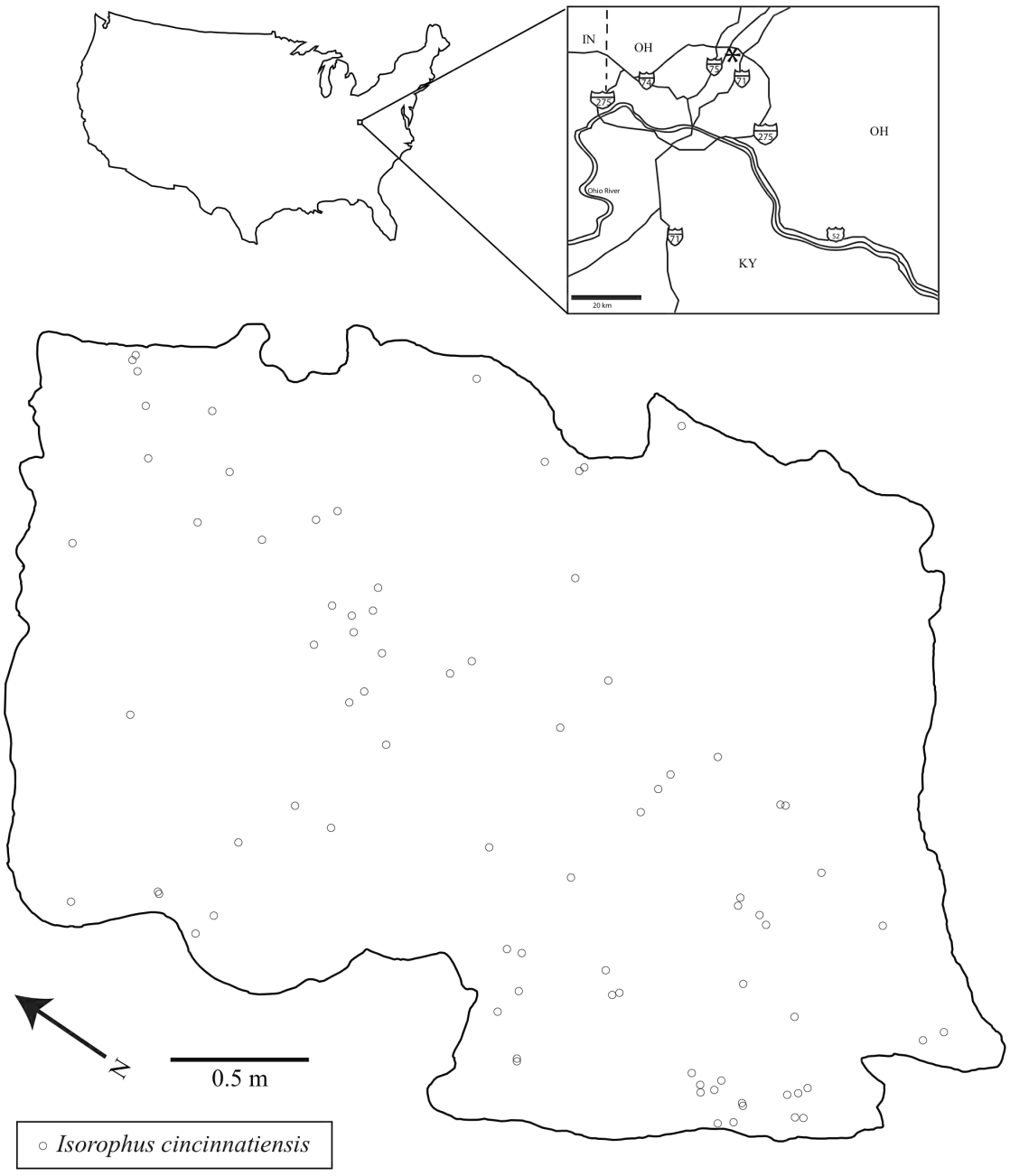

FIGURE III-3 – Map showing location of edrioasteroids on the Sharonville mollusc pavement. Asterisk on map insert shows location where pavement was collected.

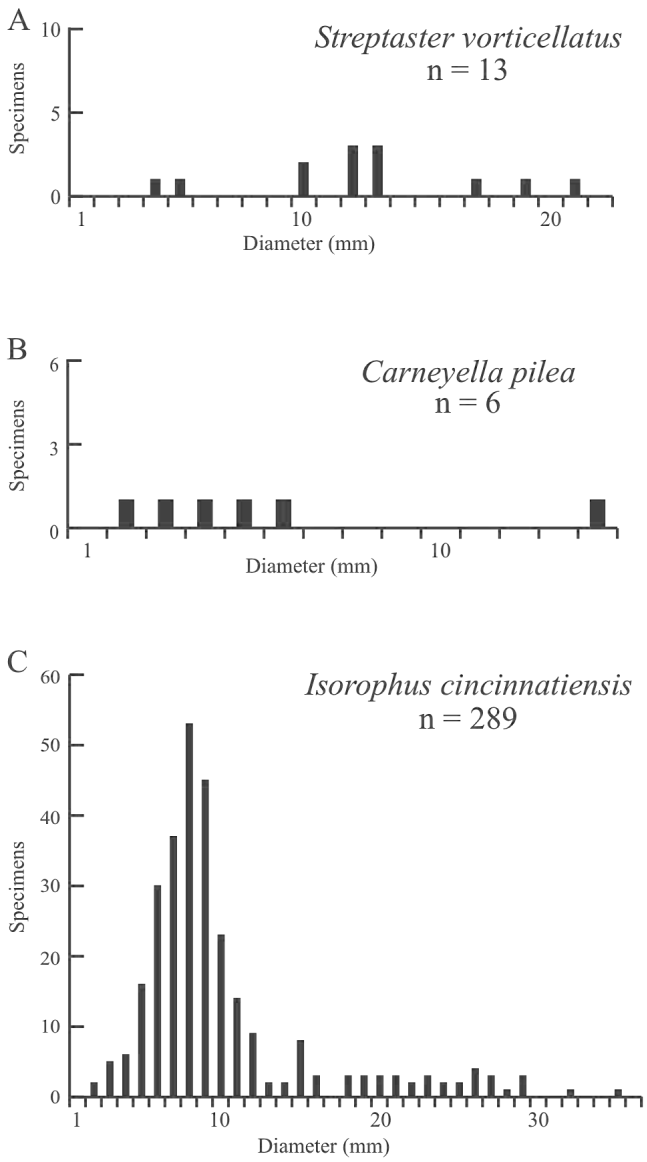

FIGURE III-4 – Population frequency distribution of edrioasteroids on the Florence pavement. A) Specimens of *Streptaster vorticellatus* show a normal distribution. B) Specimens of *Carneyella pilea* had too few specimens for meaningful analysis. C) Strong right-skewed distribution of *Isorophus cincinnatiensis* suggests species may have been an r-strategist. Strong modal peak at 6-8 mm suggests spatfall prior to entombment.

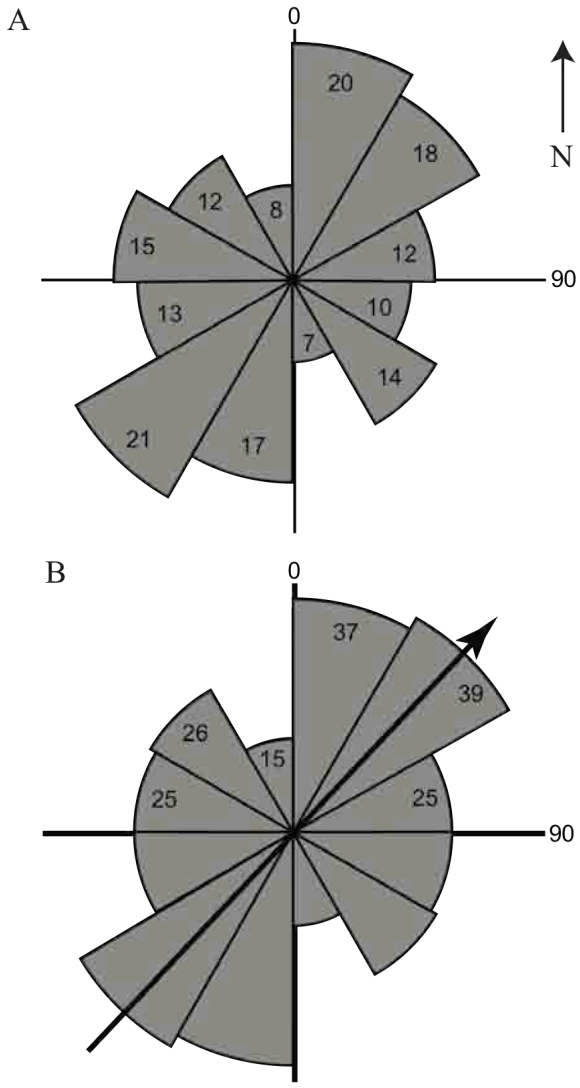

FIGURE III-5 – Orientation of edrioasteroid fauna on the Florence pavement. A) Vector analysis for *Isorophus cincinnatiensis* shows no preferential orientation exists. B) Bipolar orientation test for *Isorophus cincinnatiensis* shows slight preferential orientation ($p = 0.054$). Arrow indicates azimuth of 43.05 degrees.

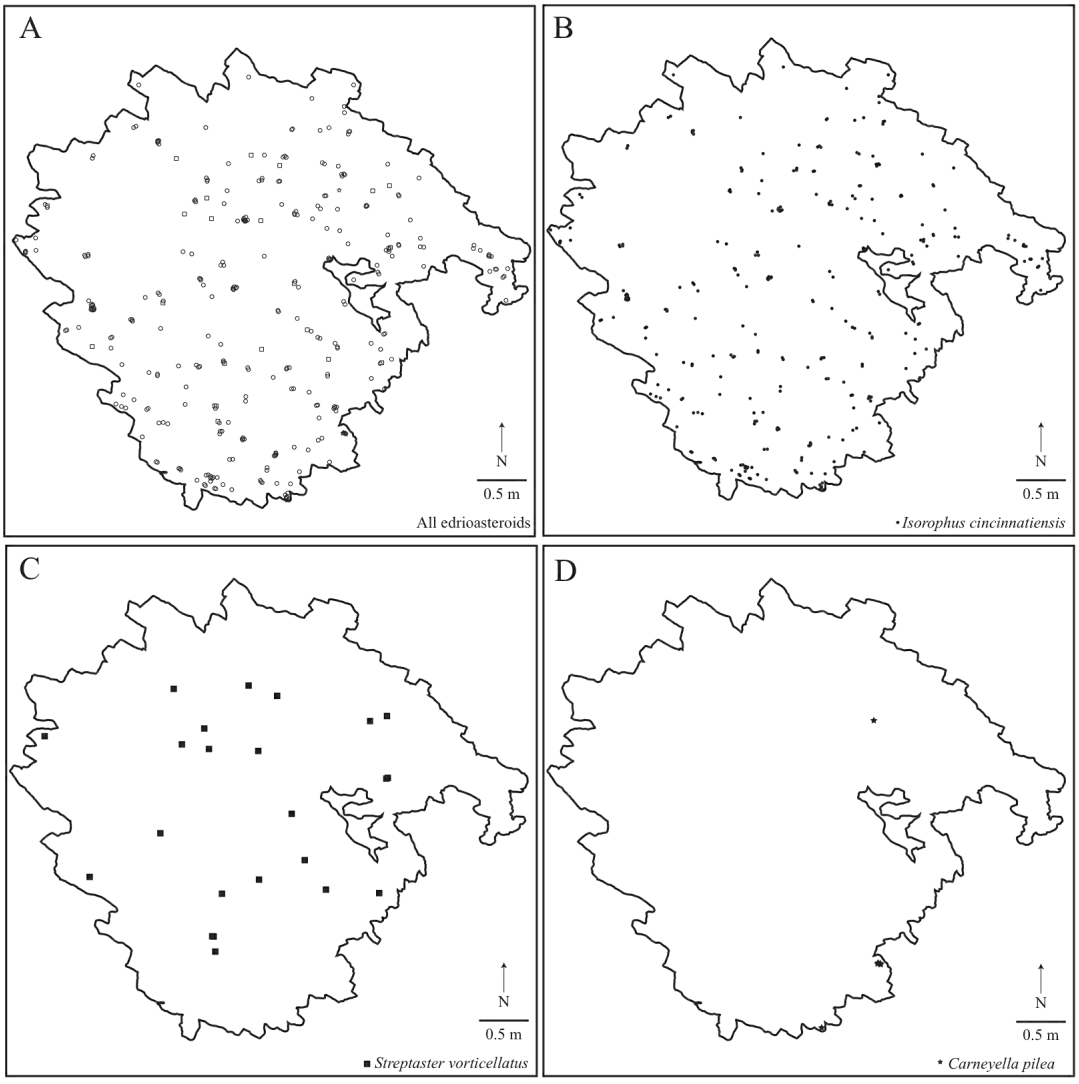

FIGURE III-6 – Maps showing edrioasteroid spatial distributions on the Florence pavement. A) Interspecific Nearest Neighbor Analysis shows the entire population of edrioasteroids is clustered on the pavement ($\overline{R}$ = 0.57). B) Specimens of *Isorophus cincinnatiensis* are clustered on the pavement ($\overline{R}$ = 0.54). C) Specimens of *Streptaster vorticellatus* are clustered on the pavement ($\overline{R}$ = 0.53). D) *Carneyella pilea* had too few specimens for Nearest Neighbor Analysis.

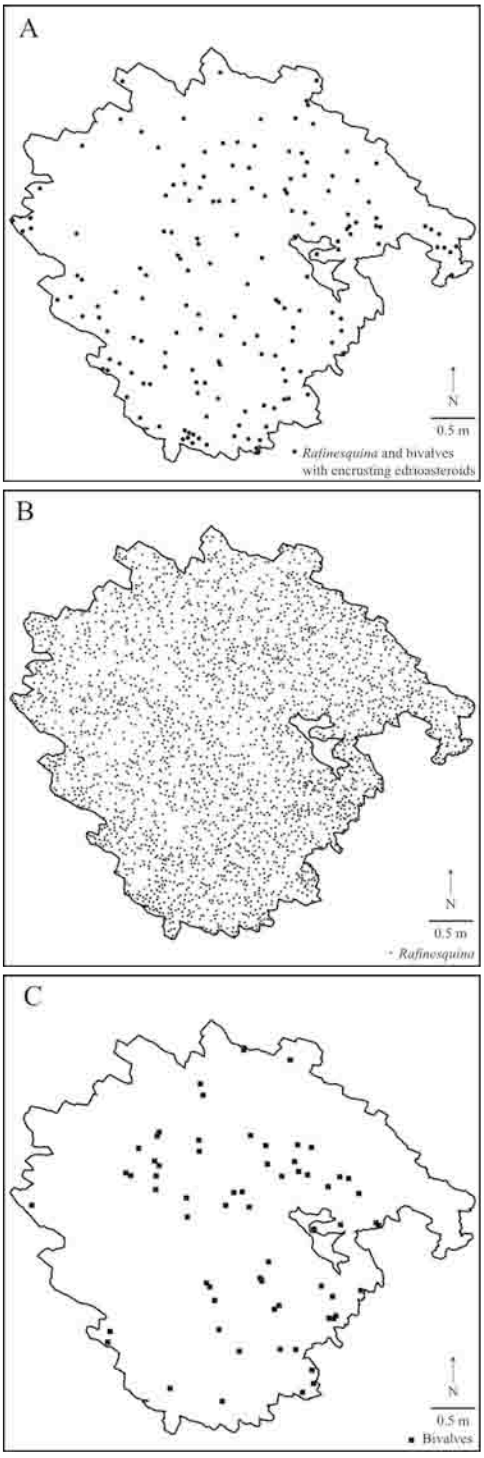

FIGURE III-7 – Maps showing spatial distribution for brachiopods and bivalves on the Florence pavement. A) *Rafinesquina* brachiopods (n = 163) and bivalves (n = 2) with encrusting edrioasteroids are random on the pavement ($\overline{R}$ - 0.97). B) The brachiopod population is slightly dispersed on the pavement ($\overline{R}$ = 1.21). C) The bivalve population is clustered on the pavement ($\overline{R}$ = 0.59).

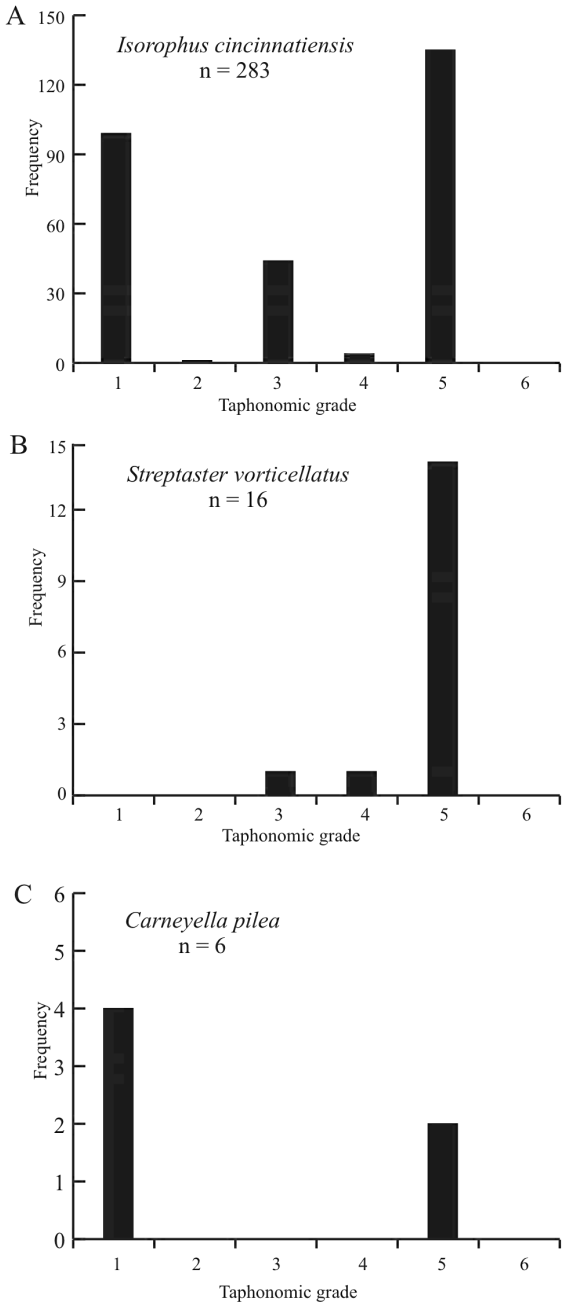

FIGURE III-8 – Histograms showing taphonomic grade of edrioasteroids found on the Florence pavement. The majority of edrioasteroid specimens fall within taphonomic grades one and five with few in categories two, three, and four. We suggest postmortem thecal bloating and rupture accounts for this pattern. Distribution of taphonomic grade for: A) *Isorophus cincinnatiensis*, B) *Streptaster vorticellatus*, and C) *Carneyella pilea*.

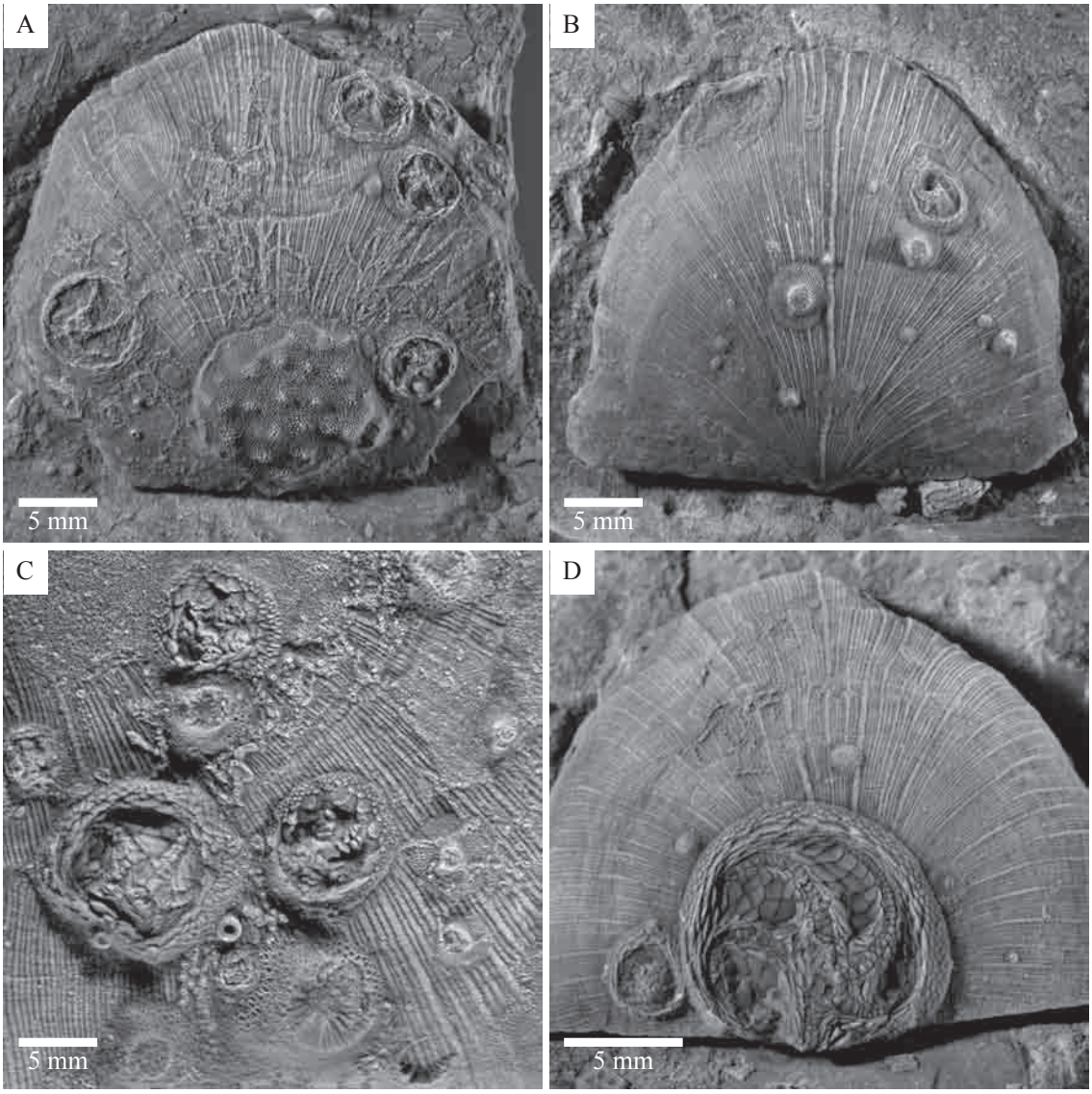

FIGURE III-9 – Faunal interactions found on the Florence pavement. A) Edrioasteroid and bryozoan interaction with 1 mm gap between the two faunal elements. Circular growth patterns of cyclostome bryozoans may indicate location of earlier encrusting edrioasteroids, B) *Isorophus cincinnatiensis* overgrowing bryozoan, C) Multiple interactions between edrioasteroids and bryozoans. Notice edrioasteroid margin deformation, and D) Two specimens of *Isorophus cincinnatiensis* displaying margin deformation at point of contact. Juvenile edrioasteroid shows flattening of the peripheral rim while peripheral rim of mature specimen is raised at a severe angle.

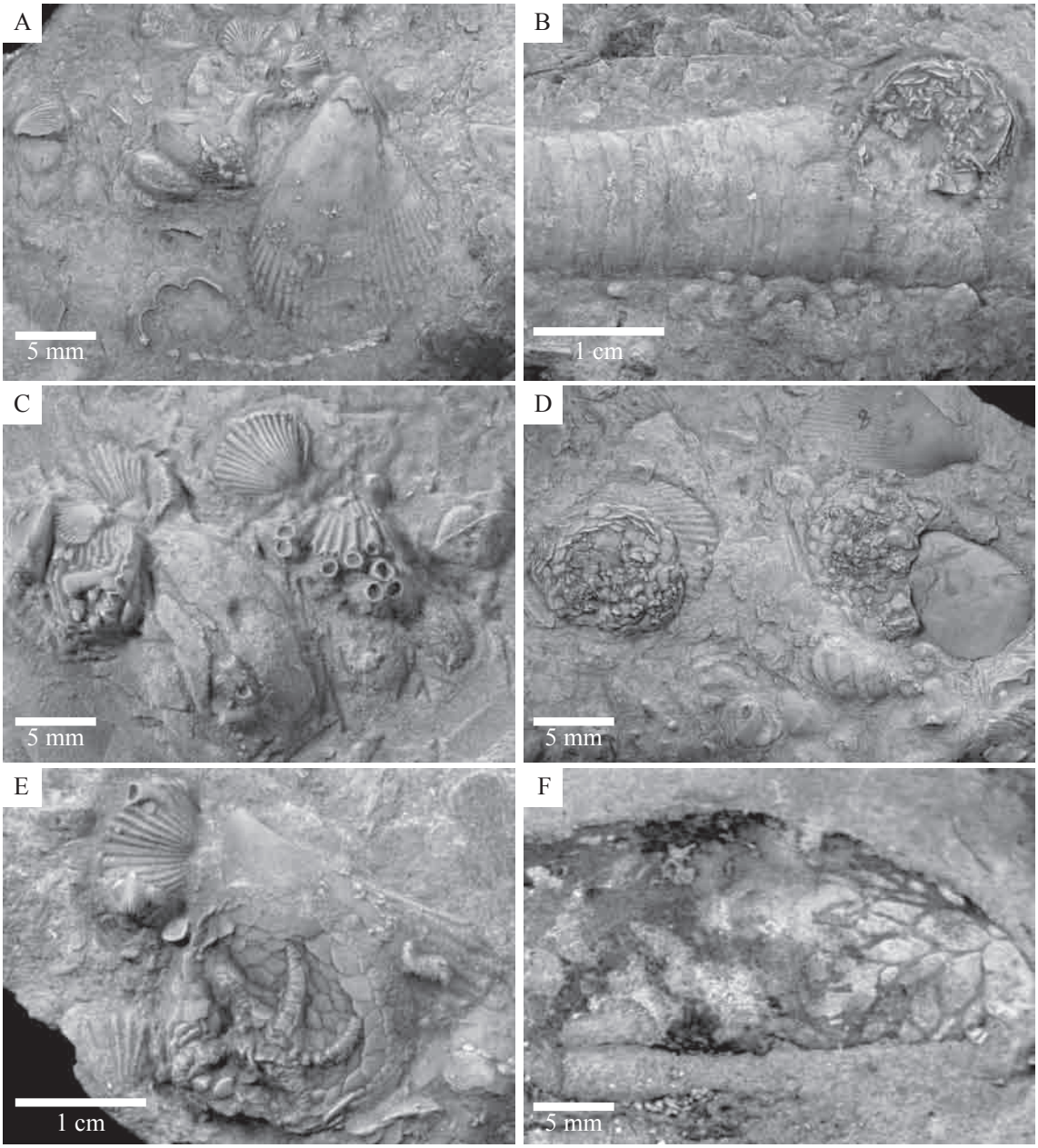

FIGURE III-10 – Fauna of the Sharonville pavement. A) Typical fauna found on surface, B) Cephalopod with encrusting *I. cincinnatiensis* edrioasteroid, C) *Zygospira* brachiopods alive on the substrate at the time of burial as evidenced by beak down life position. Notice *Cornulites* worm tubes growing upward on *Zygospira* brachiopods, D) Specimens of *Isorophus cincinnatiensis* encrusting the bivalves *Ambonychia* and *Modiolopsus*, E) Typical *Isorophus cincinnatiensis* edrioasteroid found attached to *Ambonychia* bivalve with apertures along commissure suggesting parasitic feeding off brachiopod currents, and F) Evidence of bryozoan encrustation inside bivalve shell indicating bivalve was dead prior to entombment.

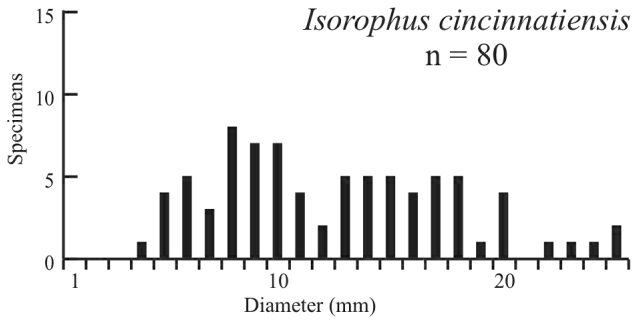

FIGURE III-11 – Population structure of *Isorophus cincinnatiensis* found on the Sharonville pavement showing a weak right-skewed distribution.

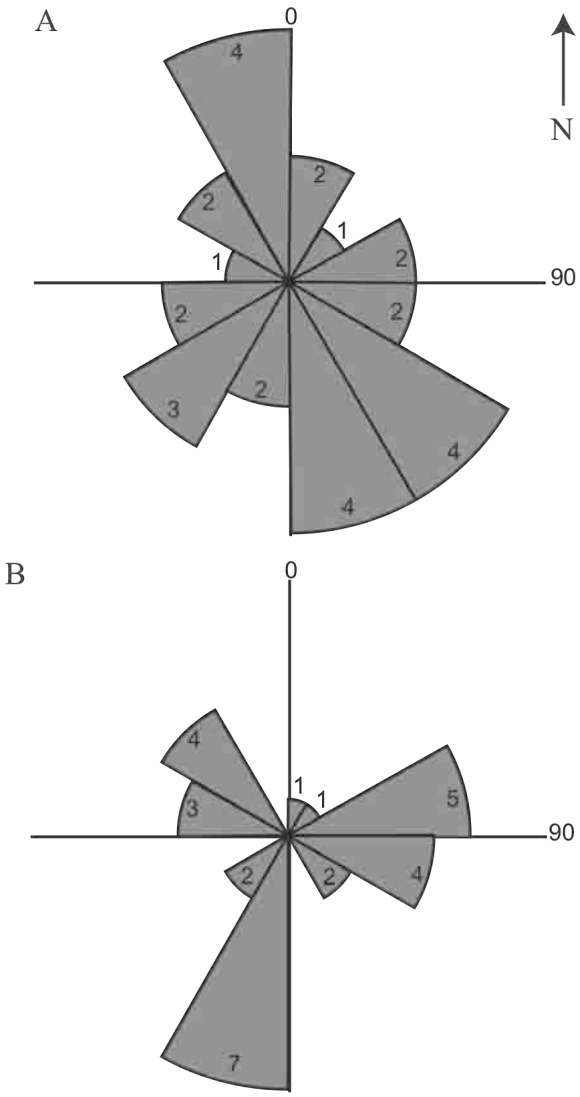

FIGURE III-12 – Edrioasteroid thecal orientation on the Sharonville pavement. A) Specimens of *Isorophus cincinnatiensis* show no preferred orientation. B) Specimens of *Ambonychia* bivalves with encrusting edrioasteroids show no preferred orientation.

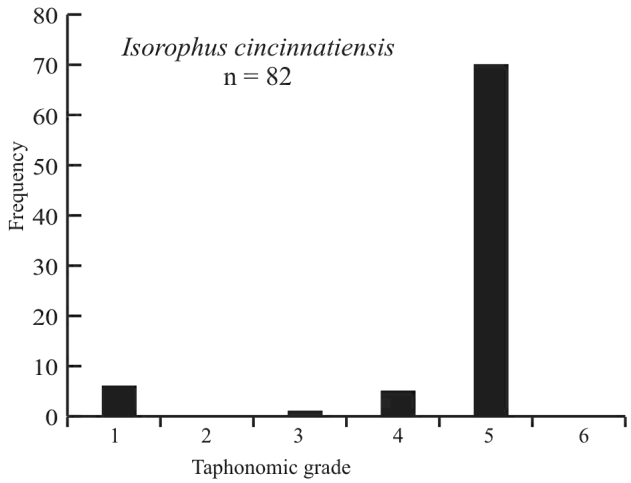

FIGURE III-13 – Taphonomic grade for specimens of *Isorophus cincinnatiensis* on the Sharonville pavement. Most edrioasteroids fall within taphonomic grade five. We suggest postmortem thecal bloating and rupture is responsible for disarticulation of the peripheral rim.

IV. THE PALEOBIOGEOGRAPHY OF ORDOVICIAN EDRIOASTEROIDS

This chapter is a reformatted version of a paper, by the same name, to be submitted to the journal Palaeogeography, Palaeoclimatology, Palaeoecology by René A. Shroat-Lewis, Colin D. Sumrall, and Michael L. McKinney.

ABSTRACT

Edrioasteroids, an extinct clade of echinoderms, have a fossil record spanning over 300 million years. Their fossil record, however, is poor because of rapid postmortem disarticulation of their multi-element skeletons. Here we examine biogeographic patterns of edrioasteroids in the Ordovician, the earliest time when they have a rich fossil record with a global distribution. Compilation and analysis of published data on the distribution of Ordovician genera indicate edrioasteroid fauna have relatively low diversity in the Early Ordovician, which increases during the Middle Ordovician. Late Ordovician edrioasteroid fauna reach their diversity apex during the Katian. Diversity drops dramatically during the Hirnantian. Ordovician edrioasteroids are known from every continent except Antarctica, Australia, South America, India, and sub-Saharan Africa. Generic and species level comparisons using Jaccard and Sørensen similarity indices show Swedish and Russian fauna show greater affinities to each other than to other biogeographic regions. Caution should be used with this interpretation, however, because only one genus is reported from each biogeographic area. Edrioasteroids were generally believed to be restricted to warm, tropical, clear water environments, mainly in Laurentia. Compilation of Gondwandan edrioasteroids, however, shows substantial diversity even at high southern paleo-latitudes. We propose that Ordovician edrioasteroids are likely more broadly distributed than presently known. Historical lack of paleontological field research, resulting from inaccessibility coupled

with sampling bias, may be contributing to our limited understanding of their global dispersal patterns.

INTRODUCTION

Edrioasteroids are an extinct clade of echinoderms that have a fossil record spanning over 300 million years, from the Early Cambrian through the Early Permian (Arendt, 1983; Sumrall, 2009). Edrioasteroid fossils are rarely preserved because postmortem decay and decomposition leads to rapid disarticulation of their multi-element skeleton (Bell, 1976; Sumrall et al., 2006). Rapid burial is an essential element for the preservation of fully articulated individuals because it entombs the organisms under a layer of sediment, removing them from the sediment/water interface and protecting them from further disruption by scavengers.

The terminology used in edrioasteroid systematics is confusing. Several names Edrioasteroidea, Edrioasterida, Edrioasteridina, *Edrioaster,* and *Edriophus*, and Isorophida, Isorophina *Isorophus*, and *Isorophusella* all have similar etymologies. See Figure IV-1 for a cladogram with these terms and the clades they circumscribe.

There are two major edrioasteroid clades (Fig. IV-1). The first, Edrioasterida, includes edrioasterins, the former class Edrioblastoidea, rhenopyrgids, and cyathocystids (Guensburg and Sprinkle, 1994). Members of this clade date from the Middle Cambrian and all but the rhenopyrgids were extinct by the end of the Ordovician. Globose or biscuit shaped, edrioasterins have wide ambulacra, a primitive anal opening and a short stalk (Fig. IV-2A). Edrioblastoids have a globular theca atop a meric stem. Rhenopyrgids have a small domal oral surface with a flexible pedunculate zone, and

cyathocystids have a domal oral surface atop a fused pedunculate zone (Guensburg and Sprinkle, 1994).

The second major clade is Isorophida, whose ancestry can be dated to the Late Cambrian (Zamora and Smith, 2010). Isorophida includes the pyrgocystids, Lebetodiscins and isorophins. Isorophid edrioasteroids commonly have a domal or clavate shaped multi-part theca (Fig. IV-2B), although discoidal and cylindrical thecae do occur (Bell, 1976). The oral surface is generally flexible and a peripheral rim acts as a holdfast. This clade comprises the vast majority of edrioasteroid taxa in Ordovician strata.

Edrioasteroids are most often associated with shallow marine carbonate environments. These taxa are obligate encrusters and attach to hardgrounds, clasts, bioclasts and shells of living organisms (Brett and Liddell, 1978; Waddington, 1980; Wilson, 1985; Meyer, 1990; Guensburg and Sprinkle, 1994; Sumrall et al., 2000; Sumrall and Zamora, 2011; Shroat-Lewis et al., 2011). Like most echinoderms, edrioasteroids probably had a brief planktonic larval stage with limited migration ability. This makes them excellent candidates for paleobiogeography studies because of their limited dispersal and local endemism.

This study summarizes paleogeographic distribution patterns of the edrioasteroids during the Ordovician. This is the earliest time where we have a rich record of edrioasteroids with a global distribution. Compilation of biogeographic data may help in interpretation of distributional patterns with respect to climate, latitude, and ocean currents; and may help predict localities where additional specimens may be found. Here

we incorporate the Jaccard and Sørensen similarity coefficients (Jaccard, 1901; Sørensen, 1948) to assess the degree of association between individuals and sites. Finally, we create individual-based species and generic accumulation curves to chart the discovery of new species and genera. Year of taxonomic publication was used as discovery date for this analysis.

ORDOVICIAN GEOGRAPHY

The Ordovician world had the greatest extent of epicontinental seas in the Phanerozoic (Jaanusson, 1984). The Panthalassic Ocean (Fig. IV-3A-C) occupied the majority of the northern hemisphere. Four large isolated continents occur in the Ordovician: Gondwana, Laurentia, Baltica, and Siberia (Cocks and Torsvik, 2007). The supercontinent Gondwana (Fig. IV-3A-C) occupied 100 degrees of paleolatitude from the South Pole to north of the equator (Cocks and Torsvik, 2004). The western portion of Gondwana included modern-day South America, Africa, Arabia, Florida, and Madagascar (Ziegler et al., 1979; Cocks and Torsvik, 2004) along with the peri-Gondwanan constituents Avalonia, SE Ireland, England, Wales, Belgium, the Netherlands, and Holland, and Perunica (modern-day Bohemia) (Cocks and Torsvik, 2004). Eastern Gondwana included India, most of Australia, Antarctica, and New Guinea (Ziegler et al., 1979; Cocks and Torsvik, 2004). Avalonia separated from Western Gondwana near the end of the Tremadocian, opening the Rheic Ocean (Fig. IV-3A-C) and beginning the eventual dispersal of the supercontinent (Scotese and McKerrow, 1990; Cocks and Torsvik, 2002; Cocks and Torsvik, 2004; Cocks and Fortney, 2009). Laurentia (Fig. IV-3A-C), which includes modern-day North America, northwest Ireland,

Scotland, Greenland, and the North Slope of Alaska and the Chukotsk peninsula of NE USSR (Scotese and McKerrow, 1990; Cocks and Torsvik, 2004), was situated on the paleoequator, northwest of the Iapetus Ocean, throughout the Ordovician. Baltica (Fig. IV-3A-C) underwent a slight counter-clockwise rotation as it moved northward from fairly high southerly paleolatitudes in the earliest Ordovician towards equatorial waters (Fig. IV-3A-C) by the Late Ordovician (Cocks and Torsvik, 2004), resulting in a change from cold to tropical seas (Dronov and Rozhnov, 2007). Baltica soft-docked with Avalonia at about 443 Ma (Cocks and Torsvik, 2004; Cocks and Fortney, 2009). Siberia (Fig. IV-3A-C) was situated equatorially during the Ordovician.

The marine biosphere underwent an exponential rise in diversity that was more rapid than at any other time during the Phanerozoic (Sepkoski, 1995). Communities filled with epifaunal suspension feeders, deep burrowers, and carnivores expanded during the Early Ordovician (Bambach, 1983; Droser and Sheehan, 1997) with more than 350 new Paleozoic Evolutionary Fauna (Paleozoic EF) families added in what Sepkoski (1981) called the "largest turnover in composition of marine faunas seen in the history of the ocean." Reef and hardground communities flourished as well, with organisms becoming more specialized as they developed narrower ecological requirements, modified their use of resources, and improved competitive abilities. Marine generic diversity during the Mid Ordovician increased three- to fourfold to approximately 1,200 genera (Webby, 2004). Paleozoic EF benthic elements, such as articulated brachiopods, cephalopods, echinoderms, and bryozoans, expanded more rapidly than the pelagic components (Webby, 2004). Biomass in the planktonic realm increased as well with the

evolution of dendroid graptolites to planktonic anisograptids. Similar patterns were seen in the evolutionary history of radiolarians (Trotter et al., 2008).

Much of the increase in diversity has been linked to changes in global climate temperatures, which affected ocean circulation patterns. Oxygen isotope composition is often used to record changes in environmental conditions and constrain paleo-ocean temperatures. Recent studies (Brenchley et al., 1994; Brenchley, 2004; Trotter et al., 2008; Finnegan et al., 2011) show a seawater cooling trend that began during the Early Ordovician, where temperatures decreased from greenhouse conditions (~42˚C) to modern equatorial temperatures (~28˚C) over the course of ~25 My. The warm waters during the Early Ordovician contributed to a sluggish shallow and deep ocean circulation pattern, reducing the degree of upwelling and nutrient supply from the deep ocean sources (Barnes, 2004). Seawater cooling through the Ordovician changed the deep ocean circulation patterns, speeding up circulation and increasing upwelling, which provided essential nutrients for organisms. Global seawater temperatures changed drastically during the Late Ordovician. Widespread glaciation and rapid ice sheet growth at the South paleopole caused sea temperatures to fall by as much as 10˚C during the latest Ordovician (Hirnantian). This temperature decrease may have resulted in substantial faunal turnovers in a biota largely adapted to warmer, more stable conditions (Cocks and Torsvik, 2002; Brenchley, 2004), and has been linked to the major mass extinction of marine life at the end of the Ordovician (Finnegan et al., 2011).

Cool climatic conditions and ocean water temperatures were characteristic for much of Gondwana, and were not conducive to carbonate hardground formation.

Although Eastern Gondwana extended to the equator and had a much more tropical environment (Cocks and Torsvik, 2002), the polar Gondwanan terrigenous sediments (Scotese and McKerrow, 1990) are where a rich echinoderm fauna has been preserved (Lefebvre and Fatka, 2003; Lefebvre et al., in press).

Hot, humid weather conditions and shallow equatorial seas surrounded the Laurentian continent (Ziegler et al., 1979). These warm carbonate-rich waters provided conditions necessary for the formation of hardgrounds and shell pavements, which then provided suitable substrate for encrusting echinoderms. Sprinkle and Guensburg (2004) assert that the Laurentian paleocontinent provided the richest echinoderm fauna found thus far, and is attributed to the carbonate-rich water and availability of hardgrounds for encrustation.

METHODS

Geographic distribution data for all known occurrences of Ordovician edrioasteroids were gathered from published faunal reports. The time scale of Walker and Geissman (2009) was used for this study. Modern day latitude and longitude coordinates for these collection sites were determined using Google Earth. The coordinates were then plotted on Mollweide Projection Maps of paleogeographic reconstructions of the Ordovician Earth using BugPlates software, generously provided by StatoilHydro.

The degree of similarity between generic and species composition was calculated using the Jaccard and Sørensen similarity indices (Jaccard, 1901; Sørensen, 1948). These indices are applied to presence/absence data, and measure the degree of overlap between

the two data sets. They were chosen because of their simplicity, widespread use, and reliance on presence/absence data. EstimateS (Version 8.2, R. K. Colwell, 2009), available free on the internet, was used to generate Jaccard and Sørensen similarity coefficients.

The Jaccard similarity coefficient is defined as:

$$C_j = \left| \frac{j}{a + b - j} \right|$$

where j = the number of genera/species found in both sites, a = the number of genera/species in Site A, and b = the number of genera/species in Site B (Magurran, 1988). The Jaccard coefficient is zero if the two sets have no common members, and is one if they are identical. Higher numbers indicate better agreement between the sets.

Like the Jaccard similarity index, the Sørensen coefficient also measures set agreement. In this case, the measure is given by the formula:

$$C_s = \left| \frac{2j}{A + B} \right|$$

where j = the number of genera/species found in both sites, a = the number of genera/species in Site A, and b = the number of genera/species in Site B (Magurran, 1988). Again, a value of zero indicates no overlap; a value of one indicates perfect alignment.

Presence/absence data were analyzed using EstimateS with the results used to construct dendrograms. Using the Jaccard Similarity Index as a guide, the most taxonomically similar areas were clustered together on the dendrogram. These two

biogeographic areas were then combined and the similarity analysis was conducted again. This process continued until only two biogeographic areas remained.

Species and generic accumulation curves were created from two sets of data: all of the edrioasteroid data points combined and data points separated by geographical region. These curves represent the "law of diminishing returns" as they tell you when to stop sampling because you've either sampled all available species or genera, or, you've sampled enough to extrapolate a good estimate of how many species or genera their might be (Dove and Cribb, 2006). In theory, the accumulation curves are initially steep at the beginning of sampling because all findings are new discoveries. Continued sampling decreases the probability of discovering new species or genera. The species accumulation curve is typically concave-down with ever decreasing slope, reaching an asymptote when the likelihood of finding a new species or genus approaches zero.

RESULTS AND DISCUSSION

Paleobiogeography of Edrioasteroids

Data on known occurrences of Ordovician edrioasteroid faunas throughout the world are summarized in Table IV-1. Our present survey records a total of 36 genera (68 species). North America has the greatest faunal diversity with generic representatives from all taxonomic groups (Fig. IV-4). These generic groups are generally evenly partitioned with 20% edrioasterida (including cyathocystids and edrioasterinids), 23% pyrgocystids, 30% lebetodiscids, and 27% isorophinids (Fig. IV-4). Prague has no reported findings of edrioasterida. Instead, this fauna is composed of 20% pyrgocystids, 20% lebetodiscids, and 60% isorophinids (Fig. IV-4). Moroccan fauna is composed of

58% pyrgocystids and 42% isorophinids while the fauna of Scotland is composed of 50% rhenopyrgids and 50% pyrgocystids albeit based on two species (Fig. IV-4). Finally, the fauna from both Sweden and Russia are composed of 100% cyathocystid Edrioasterids (a single species) (Fig. IV-4).

Early Ordovician Fauna: Tremadocian – Floian (488 – 472 Ma)

There are few edrioasteroids reported at the beginning of the Ordovician, and are restricted to samples from North America (Guensburg and Sprinkle, 1994) and Morocco (Sumrall and Zamora, 2011). In the Tremadocian (Fig. IV-5), *Paredriophus elongatus*, an edrioasterinid edrioasteroid from Western Utah (Guensburg and Sprinkle, 1994), is the only known edrioasteroid. Floian Stage edrioasteroids (Fig. IV-6) include the edrioblastoid *Lampteroblastus hintzei* from Utah (Guensburg and Sprinkle, 1994), and the Moroccan pyrgocystid *Argodiscus espilezi* and isorophinid *Anedriophus moroccoensis* (Sumrall and Zamora, 2011). Although faunal reports are sparse for the Early Ordovician, it is important to note that each of the major clades (Edrioasterida, Pyrgocystidae, and Isorophida) is represented.

Middle Ordovician Faunas: Dapingian – Darriwilian (472 – 461 Ma)

Three edrioasteroid species have been described from Dapingian (Fig. IV-7) age rocks from Utah. These recorded specimens include the pyrgocystids *Archaepyrgus anitae* and *Fanulodiscus crystalensis*, and the isorophinid *Deltadiscus superbus* (Guensburg and Sprinkle, 1994).

Five edrioasteroid genera have been described from Darriwilian age rocks (Fig.

IV-8). The pyrgocystid *Argodiscus rarus* makes an appearance in the Prague basin during this interval (Plas and Prokop, 1979). The cyathocystid *Cyathotheca suecica* is first recorded in Darriwilian-aged rocks from European Russia (Regnéll, 1966). The lebetodiscid *Cryptogoleus youngi* is found in Ontario, Canada (Bell, 1976), while the cyathocystid *Cyathocystis americanus* and the lebetodiscid *Carneyella valcourensis* are found in rocks from Tennessee and New York, United States respectively (Bell 1976, 1982). Diversity increases during this time with the addition of seven genera previously unseen. Representatives of *Argodiscus* are found in both the Moroccan fauna (during the Early Ordovician) and the Prague fauna (during the Middle Ordovician).

Late Ordovician Faunas: Sandbian – Hirnantian (461 – 444 Ma)

Late Ordovician edrioasteroid faunas recorded the largest increase in diversity (Fig. IV-9). Diversity increases from nine genera during the Middle Ordovician to 13 during the Sandbian (Fig. IV-10). The lebetodiscid, *Foerstediscus,* pyrgocystid *Pyrgocystis* (Bell, 1982), edrioasterinid *Edriophus* (Bell, 1982) and edrioblastoid *Astrocystites* (Sprinkle, 1982) dominate the North American Sandbian fauna. Additionally, the North American fauna includes the cyathocystid *Cyathocystis* (Bell, 1982), the isorophinids *Isorophusella* (Waddington, 1980) and *Thresherodiscus* (Sumrall and Gahn, 2006), and the pyrgocystid *Pyrgocystis* (Regnéll, 1966). Peri-Gondwanan faunas include the pyrgocystid *Belochthus*? and the isorophinid *Isorophus* (Sumrall and Zamora, 2011) from Morocco, the pyrgocystid *Argodiscus* (Prokop, 1965), the undescribed isorophinid genus A ("*Agelacrinites*") (Barrande, 1887), and the lebetodiscid genus B ("*Hemicystites*") (Prokop, 1965) from the Prague Basin.

Edrioasteroids reach their diversity apex of 24 genera during the Katian (Fig. IV-9). Katian Stage genera are well known from a variety of localities (Fig. IV-11) with the most diverse fauna found on the North American continent, including specimens from Iowa (Bell et al., 1976; Kolata et al., 1987), Kentucky (Whiteaves, 1897; Bell, 1976; Sumrall, 2010), Ohio (Bell, 1976), Indiana (Bell, 1976), Illinois (Bell, 1976; Guensburg, 1988), Michigan (Bell, 1976), Tennessee (Bell, 1976), and Minnesota (Regnéll, 1966; Bell, 1976). The North American fauna is dominated by isorophids, especially the lebetodiscids *Carneyella* (Bell, 1976; Sumrall, 2010), *Lebetodiscus* (Bell, 1976), and *Cryptogoleus* (Bell, 1976), the isorophinids *Isorophus* (Bell, 1976; Bell et al., 1976) and *Isorophusella* (Bell, 1976), and the pyrgocystids *Streptaster* (Bell, 1976) and *Cystaster* (Bell, 1976). Additionally, Katian aged edrioasteroids have been documented in eastern Canada (Whiteaves, 1897; Bell, 1976), Scotland (Smith, 1980), Prague (Barrande, 1887), and Morocco (Sumrall and Zamora, 2011; in press).

The only documented Hirnantian (Fig. IV-12) edrioasteroid is the Swedish cyathocystid, *Cyathotheca* (Regnéll, 1945). This extreme drop in diversity mimics that observed in most groups of organisms during a two-phase extinction event recorded during this time. The first phase of extinction, at the beginning of the Hirnantian, saw a large fall in diversification in most taxonomic groups. Few groups, like the conodonts, survived the first phase of extinction only to suffer large losses during the second phase. Jablonski (1991) estimates that overall diversity of species decreased by 85%, and genera by 61% of genera during the Hirnantian. These losses are attributed to extreme climate change associated with the Hirnantian glaciation.

Geographic Similarity

Cluster analysis of the genera (Fig. IV-13A) present in each of the six biogeographic regions (Prague, Morocco, North America, Sweden, Russia, and Scotland) suggests the Sweden and Russia fauna are most similar in that they share one genus, *Cyathotheca*. Jaccard and Sørensen Indices gives a similarity coefficient of 1.0 (Table IV-2). Although this number indicates complete (100%) similarity, this result is misleading as both Sweden and Russia lack diversity, having only one described genus each. Morocco and Prague are next in similarity, sharing 2 genera, *Argodiscus* and *Isorophusella*. Analysis of similarity gives a similarity coefficient of 0.153 for Jaccard and 0.267 for Sørensen (Fig. IV-13A). The Morocco/Prague group is next most similar with North America, which share four genera, *Belochthus*, *Isorophus*, *Isorophusella*, and *Streptaster*. The Jaccard similarity coefficient is 0.117 and the Sørensen similarity coefficient is 0.210 (Fig. IV-13A). Further, no generic similarities exist between the Morocco/Prague/North America group the Sweden/Russia group, and Scotland (Fig. IV-13A). Species cluster analysis (Table IV-3; Fig. IV-13B) shows Sweden and Russia fauna are most taxonomically similar with one shared species, *Cyathotheca suecia*. Jaccard and Sørensen similarity coefficients indicate that no further taxonomic similarity exists between any of the geographical areas (Fig. IV-13B).

Although Jaccard's similarity index is highest for genera found in Sweden and Russia, caution should be used with this result as only one genus is represented in these two localities. Instead, we suggest that the strongest affinity lies between North America and Morocco, sharing four genera, *Belochthus*, *Isorphus*, *Isorophusella*, and *Streptaster*

during the Katian. However, the Laurentian and Moroccan land masses are separated by great distances, and an ocean, throughout the Ordovician. Edrioasteroid larva would not have been able to cross the ocean, suggesting Laurentia and Morocco must have had some method for faunal interchange prior to the Katian. We suggest that this may have occurred during the Cambrian when the two landmasses were closer together.

The Jaccard and Sørensen similarity indices assume that the data are a true and complete representation of the assemblage composition. Although edrioasteroid diversity increases dramatically during the Middle/Late Ordovician, the results of the indices show low levels of similarity, suggesting that these are single point occurrences with a substantial number of rare species. We contend that the results likely underestimate the true similarity because of the high incidence of rare species, and do not account for "unseen" shared species. Thus, we conclude that these results likely do not reflect the true diversity because the examined areas are undersampled.

Generic and Species Accumulation Curves

Figures IV-14 and IV-15 show accumulation curves for all known occurrences of edrioasteroid species and genera regardless of geographic region. Both curves show an upward trend with few plateaus. Recent fieldwork by Sumrall and Zamora (2007, 2010, 2011) has resulted in the discovery of nine new species and two new genera in Morocco and accounts for the spike at the end of the species and generic charts. These upward trending curves do not reach an asymptote, indicating that the Ordovician edrioasteroids remain undersampled.

Figures IV-16 and IV-17 show accumulation curves for known occurrences of edrioasteroid species and genera by geographic region. The species and generic richness varied between biogeographic regions, with the majority of edrioasteroids known from North America. The greatest increase in species and generic diversity occurs in Morocco where first known edrioasteroid occurrence is documented by Regnéll in 1966. The curve remains at a plateau until 2010 when recent fieldwork by Sumrall and Zamora (2010, 2011) increases the number of species and genera to 10 each. The species and generic accumulation curves for Prague, Russia, Sweden, and Scotland have reached plateaus. However, we suggest that the lack of fieldwork in these areas contributes greatly to the low diversity shown by these curves. We suggest that continued fieldwork is necessary to improve our understanding of edrioasteroid diversity.

CONCLUSIONS

Paleobiogeographic studies are based on the degree generic or species similarity between different geographic areas. Spatial distribution patterns give us insight into the biological, geographic, and climatic conditions that govern the organisms' distribution, and of how the biota and Earth have evolved together. Paleobiogeography, which uses fossils to uncover distributional patterns, is limited by the strengths and weaknesses of the fossil record.

Our findings show that of 36 Ordovician genera, 21 are known only from North America. Although the paucity of Ordovician edrioasteroid specimens outside of North America may truly reflect their rarity, with sparsely but broadly distributed population, we propose that Ordovician edrioasteroids are likely more common than previously

reported. A historical lack of paleontological field research resulting from inaccessibility coupled with sampling bias may be contributing to our limited understanding of their global dispersal patterns. Over the last few years, collections and field observations from China (Zhao et al., 2010) Morocco (Klug et al., 2008; Sumrall and Zamora, 2011, in press) and South America (Sumrall et al., 2008) have greatly increased our understanding of edrioasteroid on a global scale. These studies have demonstrated that the fauna from these areas is present, but relatively unknown. These recent discoveries suggest that additional fieldwork will likely enhance the faunal record from these seemingly deficient areas.

SUMMARY

1. Edrioasteroids reached their maximum diversity of 24 genera during the Katian.
2. There is some overlap of taxa between the equatorial and polar locations.
3. Isorophinids and edrioasterinids, with few pyrgocystids, make up the majority of edrioasteroids in the equatorial regions.
4. Pyrgocystids, with few isorophinids and no edrioasterids, make up the majority of edrioasteroids in the polar regions.
5. Edrioasteroids require hard substrate for settlement with North American fauna utilizing carbonate hardgrounds and shell pavements and Southern peri-Gondwanan fauna utilizing shell pavements.
6. Edrioasteroids were thought to be restricted to warm, tropical, clear water environments, mainly in Laurentia. However, Gondwandan diversity is high

during the Ordovician at high southern paleo-latitudes in siliciclastic environments.

7. New genera recently described from Morocco indicate that additional fieldwork in depauperate areas will likely enhance the faunal record in previously unsampled areas.

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APPENDIX IV

TABLE IV-1 – Listing of all known Ordovician edrioasteroid occurrences by Stage. Latitude and longitude are modern day coordinates.

Number on Map	Genus	Species	Location	Stage	Latitude	Longitude
1	*Paredriophus*	*elongatus*	Utah	Tremadocian	38.27	-113.31
2	*Anedriophus*	*moroccoensis*	Morocco	Floian	30.20	5.50
2	*Argodiscus*	*espilezi*	Morocco	Floian	30.20	5.50
3	*Lampteroblastus*	*hintzei*	Utah	Floian	38.41	-113.10
4	*Archaepyrgus*	*anitae*	Utah	Dapingian	38.29	-113.26
4	*Deltadiscus*	*superbus*	Utah	Dapingian	38.29	-113.26
4	*Fanulodiscus*	*crystalensis*	Utah	Dapingian	38.59	-112.20
5	*Cyathocystis*	*americanus*	Tennessee	Darriwilian	35.57	-83.55
6	*Carneyella*	*valcourensis*	New York	Darriwilian	44.36	-73.26
6	*Cryptogoleus*	*youngi*	Ontario	Darriwilian	44.30	-79.00
7	*Cyathotheca*	*suecica*	Russia	Darriwilian	59.56	30.18
8	*Argodiscus*	*rarus*	Prague	Darriwilian	49.26	12.47
9	*Pyrgocystis*	*sardesoni*	Iowa	Sandbian	42.00	-90.50
9	*Pyrgocystis*	*sardesoni*	Illinois	Sandbian	42.30	-90.38
10	*Astrocystites*	*ottawaensis*	Oklahoma	Sandbian	34.00	-97.11
10	*Cyathocystis*	*americanus*	Oklahoma	Sandbian	34.05	-97.11
10	*Cyathocystis*	*americanus*	Oklahoma	Sandbian	34.10	-97.08
10	*Cyathocystis*	*americanus*	Oklahoma	Sandbian	34.14	-96.48
10	*Cyathocystis*	*americanus*	Oklahoma	Sandbian	34.27	-97.09
10	*Cyathocystis*	*americanus*	Oklahoma	Sandbian	34.34	-96.31
10	*Cyathocystis*	*americanus*	Oklahoma	Sandbian	34.35	-96.38
10	*Edriophus*	*laevis*	Oklahoma	Sandbian	34.26	-97.08
10	*Foerstediscus*	*splendens*	Oklahoma	Sandbian	34.21	-96.57
10	*Foerstediscus*	*splendens*	Oklahoma	Sandbian	34.25	-97.11
10	*Foerstediscus*	*splendens*	Oklahoma	Sandbian	34.27	-97.09
10	*Pyrgocystis*	Sp A	Oklahoma	Sandbian	34.14	-96.48
10	*Pyrgocystis*	Sp A	Oklahoma	Sandbian	34.20	-97.08
10	*Pyrgocystis*	Sp A	Oklahoma	Sandbian	34.21	-97.17
10	*Pyrgocystis*	Sp B	Oklahoma	Sandbian	34.05	-97.11
11	*Cyathocystis*	*americanus*	Tennessee	Sandbian	35.57	-83.55
12	*Isorophusella*	*incondita*	Ontario	Sandbian	44.29	-79.09
12	*Thresherodiscus*	*ramosus*	Ontario	Sandbian	44.32	-79.10
13	*Belochthus*	*chauveli*	Morocco	Sandbian	30.20	5.50
13	*Isorophus*	*africanus*	Morocco	Sandbian	30.20	5.50
14	*Argodiscus*	*hornyi*	Prague	Sandbian	49.55	14.13
14	N. Gen. A	*bohemicus*	Prague	Sandbian	50.50	14.24
14	N. Gen. A	*confertus*	Prague	Sandbian	50.05	14.24
14	N. Gen. A	*tener*	Prague	Sandbian	50.05	14.24
14	N. Gen. A	*velatus*	Prague	Sandbian	50.05	14.24
14	N. Gen. A	*bohemicus*	Prague	Sandbian	49.55	14.13
15	*Floridiscus*	*girvanensis*	Girvan, Scotland	Katian	55.14	-4.51
15	*Rhenopyrgus*	*grayae*	Girvan, Scotland	Katian	55.14	-4.51
16	*Edrioaster*	*bigsbyi*	Michigan	Katian	45.44	-87.03
17	*Isorophusella*	*pleiadae*	Quebec	Katian	49.32	-62.57
18	*Carneyella*	*pilea*	New York	Katian	42.56	-74.08
18	*Edriophus*	*saratogensis*	New York	Katian	43.00	-73.44

TABLE IV-1 – continued

Number on Map	Genus	Species	Location	Stage	Latitude	Longitude
18	*Isorophusella*	*incondita*	New York	Katian	43.44	-75.28
18	*Isorophusella*	*trentonensis*	New York	Katian	43.16	-75.09
19	*Isorophusella*	*simplex*	Prague	Katian	50.05	14.24
19	N. Gen. B	*bellulus*	Prague	Katian	50.05	14.24
19	N. Gen. B	*latiusculus*	Prague	Katian	50.05	14.24
20	*Euryeschatia*	*reboulorum*	Morocco	Katian	29.01	10.24
20	*Moroccopyrgus*	*matacarros*	Morocco	Katian	29.01	10.24
20	*Panidiscus*	*tamiformis*	Morocco	Katian	29.01	10.24
20	*Streptaster*	*nodosis*	Morocco	Katian	29.01	10.24
21	*Isorophusella*	*gutii*	Morocco	Katian	31.31	5.31
21	*Spinadiscus*	*lefebvrei*	Morocco	Katian	31.08	4.51
21	*Streptaster*	*nodosis*	Morocco	Katian	31.12	4.49
21	*Streptaster*	*nodosis*	Morocco	Katian	31.26	4.14
21	*Streptaster*	*nodosis*	Morocco	Katian	31.31	5.31
22	*Euhydrodiskos*	*diktyotos*	Illinois	Katian	37.13	-89.27
22	*Foerstediscus*	*splendens*	Illinois	Katian	37.13	-89.27
22	*Hystrichopsydrax*	*sandersi*	Illinois	Katian	37.13	-89.27
22	*Isorophusella*	*incondita*	Illinois	Katian	37.13	-89.27
22	*Savagella*	*illinoiseneis*	Illinois	Katian	37.13	-89.27
23	*Carneyella*	*faberi*	Ohio	Katian	39.06	-85.16
23	*Carneyella*	*pilea*	Ohio	Katian	38.48	-84.12
23	*Carneyella*	*pilea*	Indiana	Katian	39.04	-85.15
23	*Carneyella*	*pilea*	Ohio	Katian	39.04	-84.20
23	*Carneyella*	*pilea*	Ohio	Katian	39.08	-84.28
23	*Carneyella*	*pilea*	Ohio	Katian	39.21	-84.07
23	*Carneyella*	*pilea*	Ohio	Katian	39.25	-84.11
23	*Carneyella*	*pilea*	Ohio	Katian	39.30	-84.44
23	*Carneyella*	*ulrichi*	Kentucky	Katian	39.53	-82.02
23	*Curvitriordo*	*shideleri*	Indiana	Katian	38.23	-85.46
23	*Cystaster*	*granulatus*	Ohio	Katian	39.04	-84.20
23	*Cystaster*	*granulatus*	Kentucky	Katian	39.05	-84.32
23	*Cystaster*	*granulatus*	Ohio	Katian	39.08	-84.28
23	*Cystaster*	*granulatus*	Ohio	Katian	39.30	-84.44
23	*Cystaster*	*stellatus*	Ohio	Katian	38.48	-84.12
23	*Cystaster*	*stellatus*	Ohio	Katian	39.04	-84.20
23	*Cystaster*	*stellatus*	Ohio	Katian	39.08	-84.28
23	*Isorophus*	*austini*	Indiana	Katian	39.04	-85.15
23	*Isorophus*	*austini*	Ohio	Katian	39.26	-83.49
23	*Isorophus*	*austini*	Ohio	Katian	39.30	-84.44
23	*Isorophus*	*austini*	Ohio	Katian	39.31	-84.05
23	*Isorophus*	*cincinnatiensis*	Indiana	Katian	39.04	-85.15
23	*Isorophus*	*cincinnatiensis*	Ohio	Katian	39.04	-84.20
23	*Isorophus*	*cincinnatiensis*	Ohio	Katian	39.08	-84.28
23	*Isorophus*	*cincinnatiensis*	Ohio	Katian	39.10	-84.05
23	*Isorophus*	*cincinnatiensis*	Ohio	Katian	39.21	-84.07
23	*Isorophus*	*cincinnatiensis*	Ohio	Katian	39.26	-84.12
23	*Isorophus*	*warrenensis*	Ohio	Katian	39.27	-84.05

TABLE IV-1 – continued

Number on Map	Genus	Species	Location	Stage	Latitude	Longitude
23	*Streptaster*	*vorticellatus*	Indiana	Katian	39.04	-85.15
23	*Streptaster*	*vorticellatus*	Ohio	Katian	39.04	-84.20
23	*Streptaster*	*vorticellatus*	Indiana	Katian	39.05	-84.50
23	*Streptaster*	*vorticellatus*	Ohio	Katian	39.08	-84.28
23	*Streptaster*	*vorticellatus*	Ohio	Katian	39.31	-84.05
23	*Streptaster*	*vorticellatus*	Ohio	Katian	39.45	-84.11
24	*Astrocystites*	*ottawaensis*	Kentucky	Katian	37.49	-84.53
24	*Carneyella*	*faberi*	Kentucky	Katian	37.59	-84.28
24	*Carneyella*	*faberi*	Ohio	Katian	38.51	-83.47
24	*Carneyella*	*pilea*	Kentucky	Katian	38.04	-84.43
24	*Carneyella*	*pilea*	Ohio	Katian	38.53	-83.30
24	*Cryptogoleus*	*chapmani*	Ohio	Katian	38.59	-82.32
24	*Curvitriordo*	*kentuckyensis*	Kentucky	Katian	38.45	-84.42
24	*Curvitriordo*	*stecki*	Kentucky	Katian	38.38	-83.44
24	*Edrioaster*	*priscus*	Kentucky	Katian	37.49	-84.53
24	*Foerstediscus*	*grandis*	Kentucky	Katian	37.49	-84.53
24	*Foerstediscus*	*grandis*	Kentucky	Katian	37.54	-84.41
24	*Lebetodiscus*	*dicksoni*	Kentucky	Katian	37.49	-84.53
24	*Streptaster*	*vorticellatus*	Kentucky	Katian	37.46	-84.23
25	*Astrocystites*	*ottawaensis*	Ottawa	Katian	45.21	-75.21
25	*Belochthus*	*orthokolus*	Ontario	Katian	45.25	-75.41
25	*Cryptogoleus*	*chapmani*	Ontario	Katian	45.25	-75.41
25	*Cryptogoleus*	*platys*	Ontario	Katian	45.25	-75.41
25	*Cryptogoleus*	*reticulatus*	Ontario	Katian	45.25	-75.41
25	*Edrioaster*	*bigsbyi*	Ontario	Katian	45.25	-75.41
25	*Isorophusella*	*incondita*	Ontario	Katian	45.25	-75.41
25	*Isorophusella*	*incondita*	Ontario	Katian	45.25	-75.41
25	*Isorophusella*	*incondita*	Quebec	Katian	45.26	-75.43
25	*Lebetodiscus*	*dicksoni*	Ontario	Katian	45.25	-75.41
25	*Lebetodiscus*	*dicksoni*	Quebec	Katian	45.26	-75.43
26	*Edriophus*	*levis*	Iowa	Katian	43.14	-91.54
26	*Isorophus*	*cincinnatiensis*	Iowa	Katian	43.14	-91.54
26	*Pyrgocystis*	*sardesoni*	Minnesota	Katian	44.00	-92.00
27	*Astrocystites*	*ottawaensis*	Iowa	Katian	42.00	-90.50
27	*Carneyella*	*pilea*	Illinois	Katian	42.27	-89.04
28	*Astrocystites*	*ottawaensis*	Ontario	Katian	44.33	-78.56
28	*Belochthus*	*orthokolus*	Ontario	Katian	44.18	-78.19
28	*Belochthus*	*orthokolus*	Ontario	Katian	44.33	-78.58
28	*Cryptogoleus*	*chapmani*	Ontario	Katian	44.18	-78.19
28	*Cryptogoleus*	*multibrachiatus*	Ontario	Katian	44.33	-78.58
28	*Cryptogoleus*	*reticulatus*	Ontario	Katian	44.18	-78.19
28	*Edriophus*	*levis*	Ontario	Katian	44.33	-78.58
28	*Foerstediscus*	*grandis*	Ontario	Katian	44.33	-78.58
28	*Isorophusella*	*incondita*	Ontario	Katian	44.18	-78.19
28	*Lebetodiscus*	*dicksoni*	Ontario	Katian	44.18	-78.19
28	*Rectitriordo*	*kirkfieldensis*	Ontario	Katian	44.33	-78.58
29	*Isorophus*	*cincinnatiensis*	Tennessee	Katian	35.09	-86.34
30	*Cyathotheca*	*suecica*	Sweden	Hirnantian	61.05	14.39

TABLE IV-2 – Number of genera shared and the Jaccard and Sørensen similarity coefficients between biogeographic regions. (Pra = Prague, Mor = Morocco, NA = North America, Swed = Sweden, Rus = Russia, Scot = Scotland)

	Pra-Mor	Pra-NA	Pra-Swed	Pra-Rus	Pra-Scot
Genera Shared	2	1	0	0	0
Unique to Prague	3	4	5	5	5
Unique to Other	8	24	1	1	2
Jaccard Index	0.153	0.034	0	0	0
Sørensen Index	0.266	0.066	0	0	0

	Mor-NA	Mor-Swed	Mor-Rus	Mor-Scot
Genera Shared	4	0	0	0
Unique to Morocco	6	10	10	10
Unique to Other	21	1	1	2
Jaccard Index	0.129	0	0	0
Sørensen Index	0.228	0	0	0

	NA-Swed	NA-Rus	NA-Scot
Genera Shared	0	0	0
Unique to N. America	25	25	25
Unique to Other	1	1	2
Jaccard Index	0	0	0
Sørensen Index	0	0	0

	Swed-Rus	Swed-Scot
Genera Shared	1	0
Unique to Sweden	0	1
Unique to Other	0	2
Jaccard Index	1	0
Sørensen Index	1	0

	Rus-Scot
Genera Shared	0
Unique to Russia	1
Unique to Other	2
Jaccard Index	0
Sørensen Index	0

TABLE IV-3 – Number of species shared and the Jaccard and Sørensen similarity coefficients between biogeographic regions. (Pra = Prague, Mor = Morocco, NA = North America, Swed = Sweden, Rus = Russia, Scot = Scotland)

	Pra-Mor	Pra-NA	Pra-Swed	Pra-Rus	Pra-Scot
Species Shared	0	0	0	0	0
Unique to Prague	8	8	8	8	8
Unique to Other	10	46	1	1	2
Jaccard Index	0	0	0	0	0
Sørensen Index	0	0	0	0	0

	Mor-NA	Mor-Swed	Mor-Rus	Mor-Scot
Species Shared	0	0	0	0
Unique to Morocco	10	10	10	10
Unique to Other	46	1	1	2
Jaccard Index	0	0	0	0
Sørensen Index	0	0	0	0

	NA-Swed	NA-Rus	NA-Scot
Species Shared	0	0	0
Unique to N. America	46	46	46
Unique to Other	1	1	2
Jaccard Index	0	0	0
Sørensen Index	0	0	0

	Swed-Rus	Swed-Scot
Species Shared	1	0
Unique to Sweden	0	1
Unique to Other	0	2
Jaccard Index	1	0
Sørensen Index	1	0

	Rus-Scot
Species Shared	0
Unique to Russia	1
Unique to Other	2
Jaccard Index	0
Sørensen Index	0

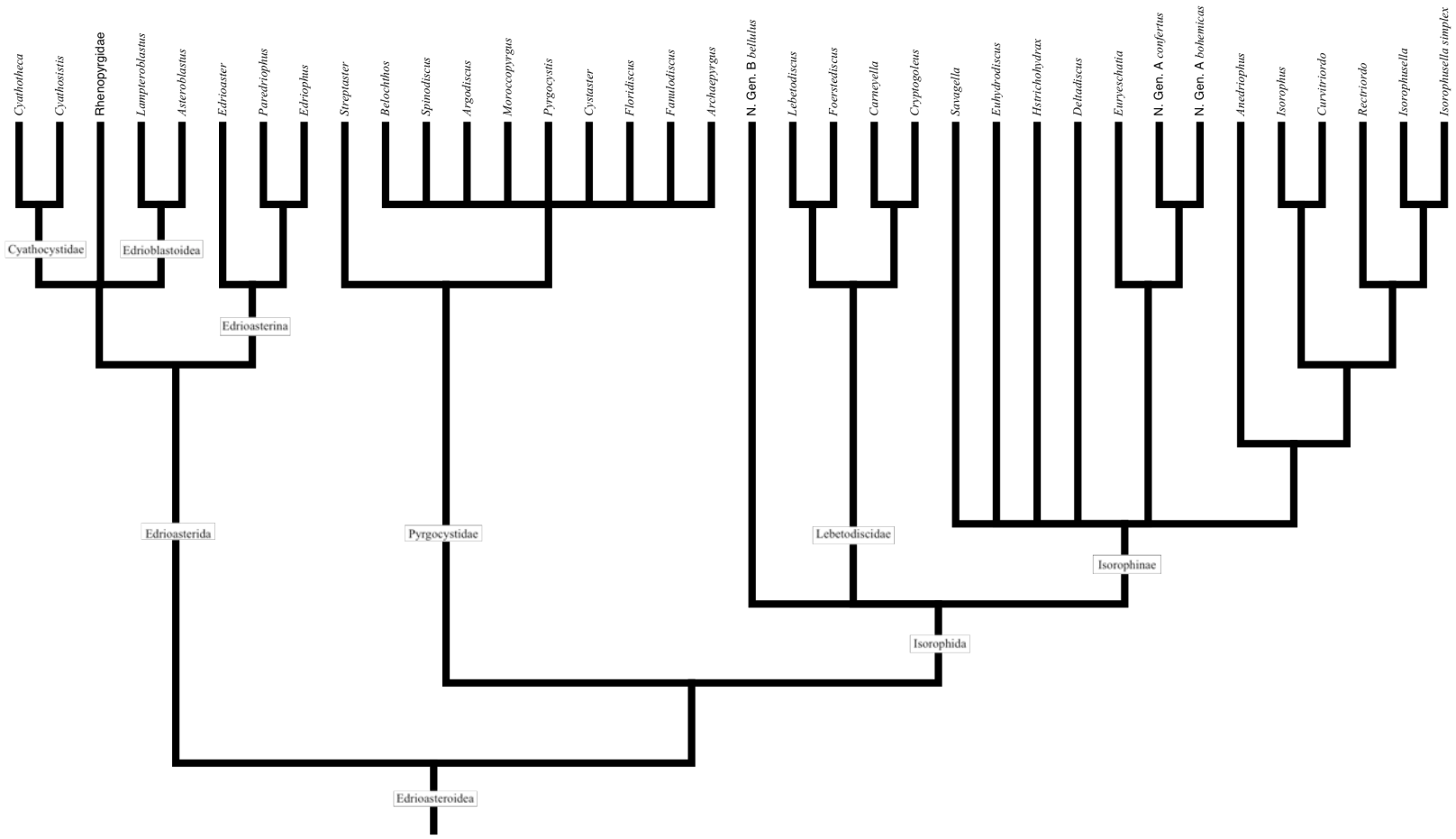


FIGURE IV-1 – Phylogentic reconstruction of Edrioasteroidea. The four major clades (Edrioasterida, Pyrogcystidae, Lebetodiscidae, and Isorophinae) are further divided to generic level.

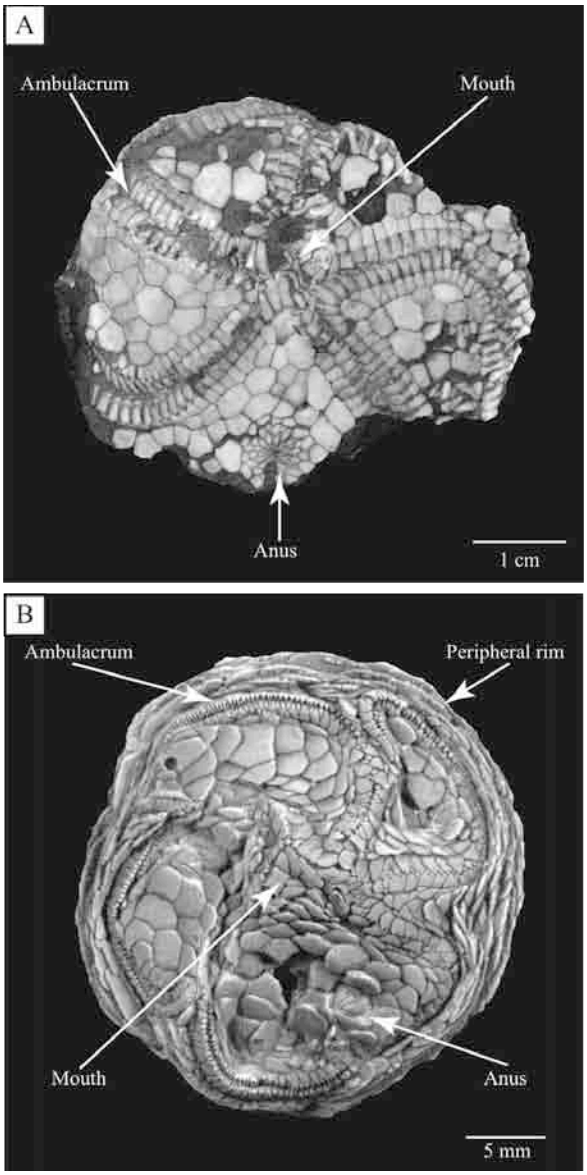


FIGURE IV-2 – Generalized edrioasteroid thecal shapes. A) Specimen of Edrioasterida, which is globose in shape. Note that ambulacra extend outward from the central mouth to the underside of the organism. B) Specimen of Isorophida. Specimen has been deflated due to sediment overburden. Ambulacra extend outwards from centrally located mouth and terminate at peripheral rim.

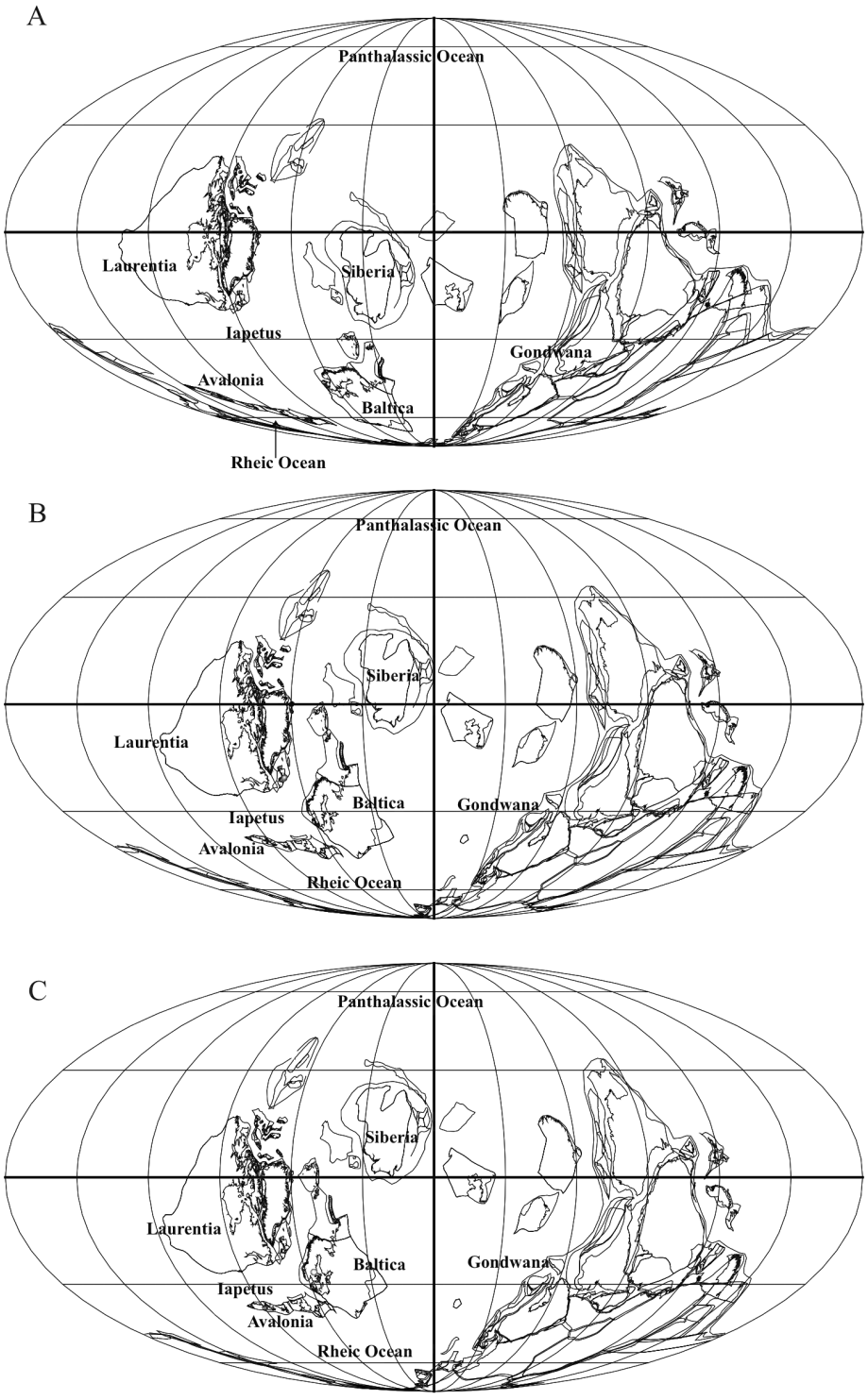


FIGURE IV-3 – Paleogeographic maps of the Ordovician to track continental movement. A) Early Ordovician, B) Middle Ordovician, and C) Late Ordovician.

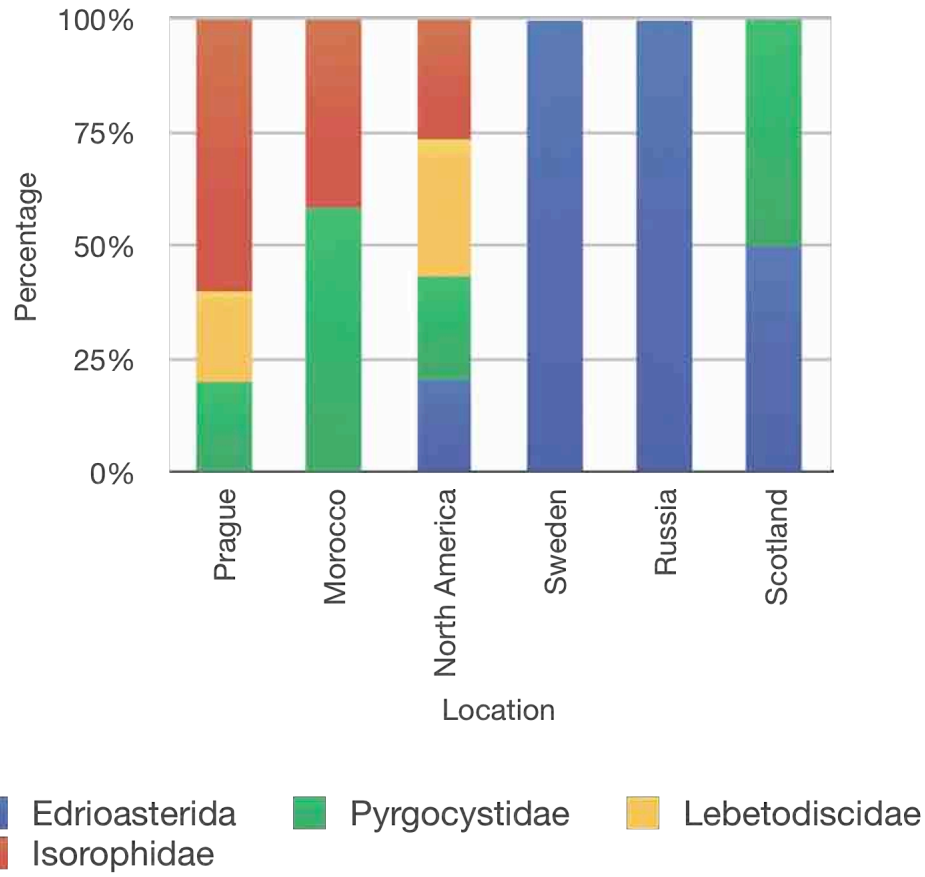
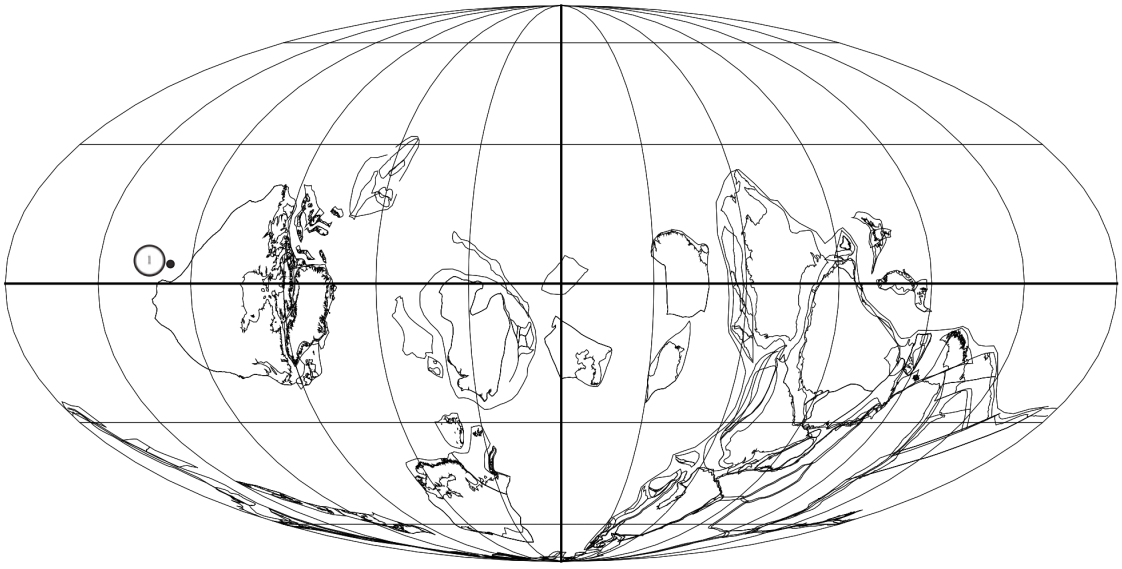
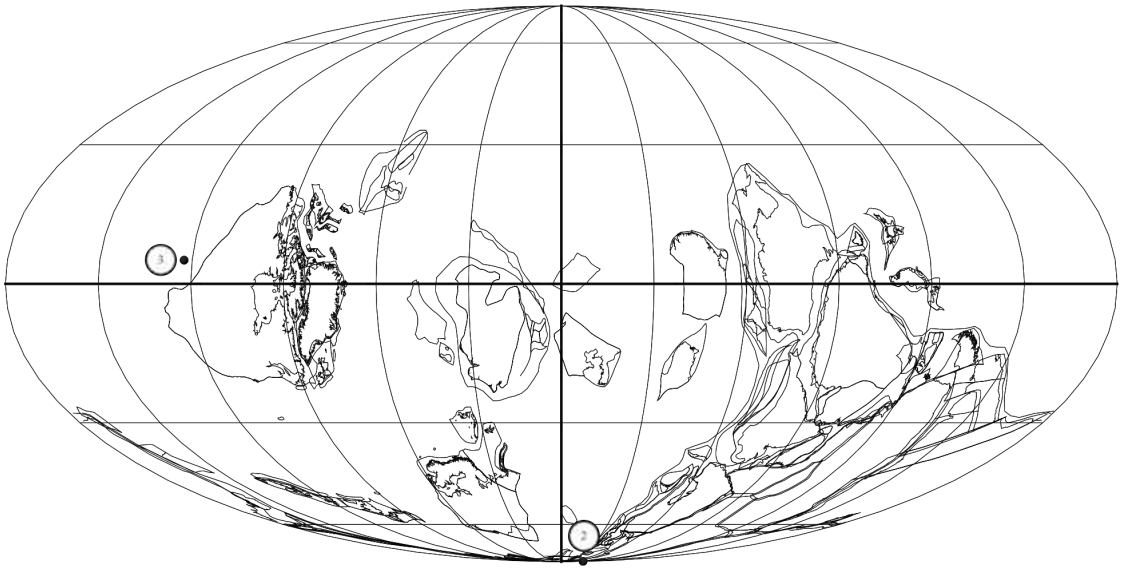


FIGURE IV-4 – Cumulative percentage of edrioasteroids found in the six biogeographic regions. North America is the only geographic location with the four major clades represented.



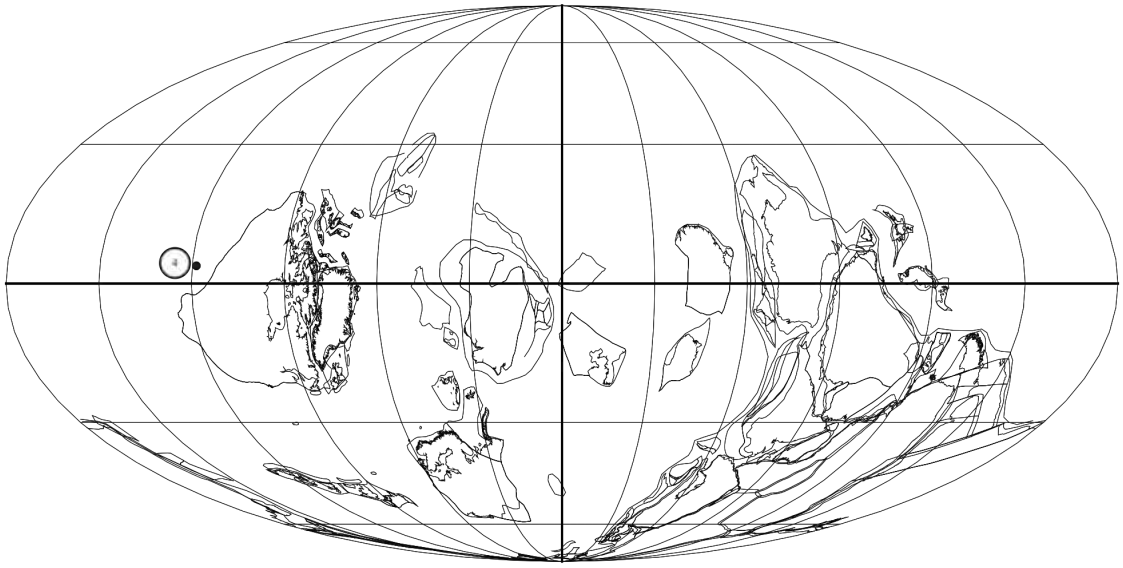
Tremadocian (488-479 Ma)

FIGURE IV-5 – Paleogeographic map of the Tremadocian. Circle indicates location of known edrioasteroid occurrences. Key can be found in Table 1.



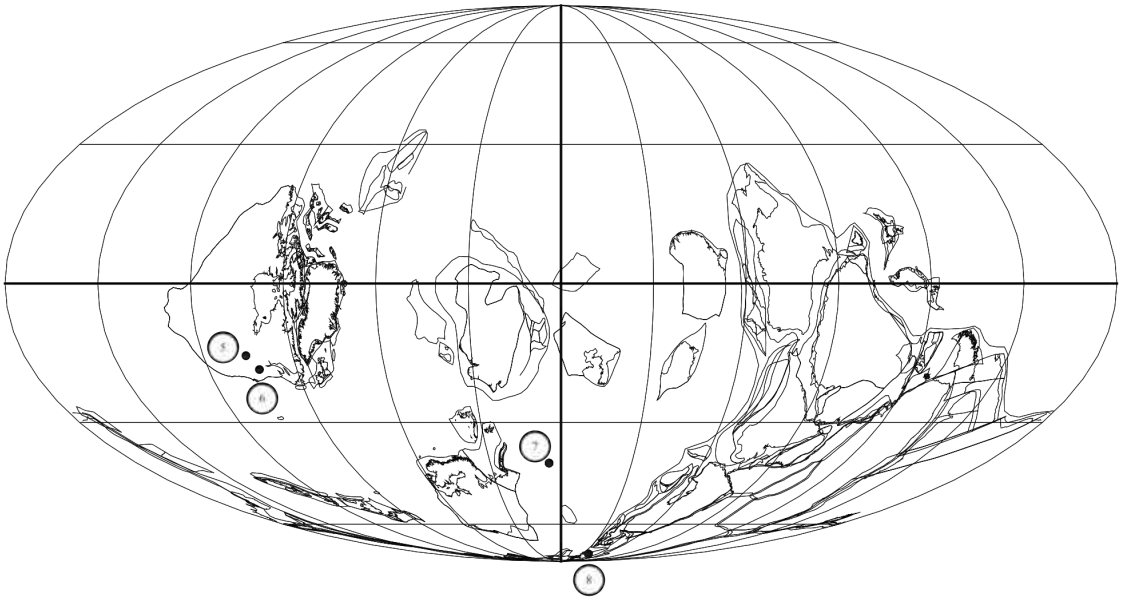
Floian (479-472 Ma)

FIGURE IV-6 – Paleogeographic map of the Floian. Circles indicate location of known edrioasteroid occurrences. Key can be found in Table 1.



Dapingian (472-468 Ma)

FIGURE IV-7 – Paleogeographic map of the Dapingian. Circles indicate location of known edrioasteroid occurrences. Key can be found in Table 1.



Darriwilian (468-461 Ma)

FIGURE IV-8 – Paleogeographic map of the Darriwilian. Circles indicate location of known edrioasteroid occurrences. Key can be found in Table 1.

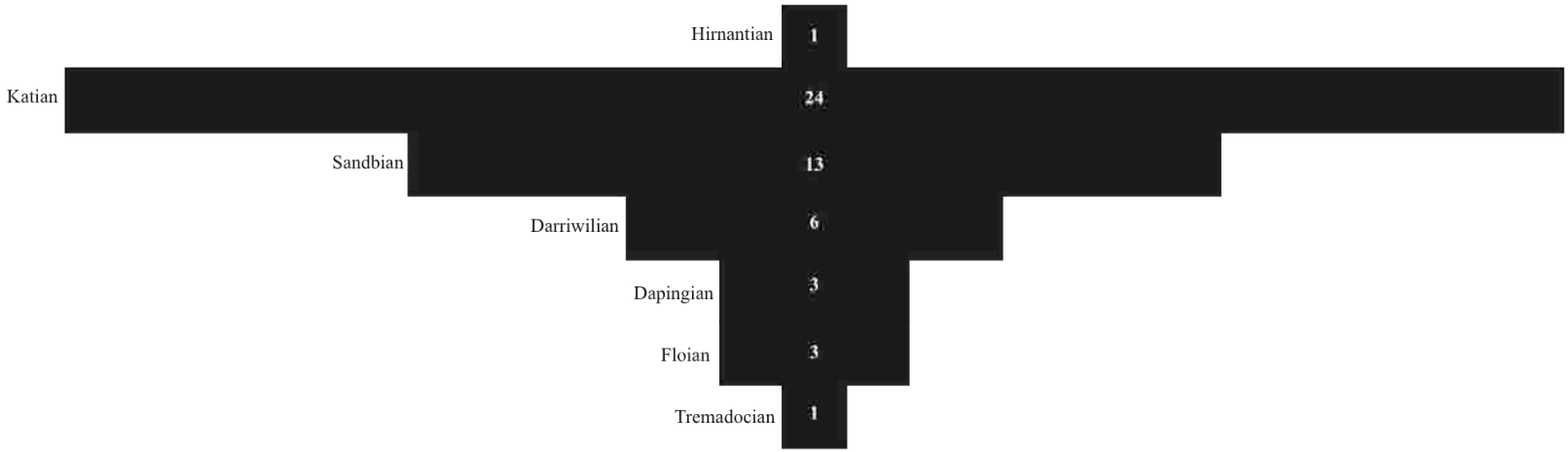
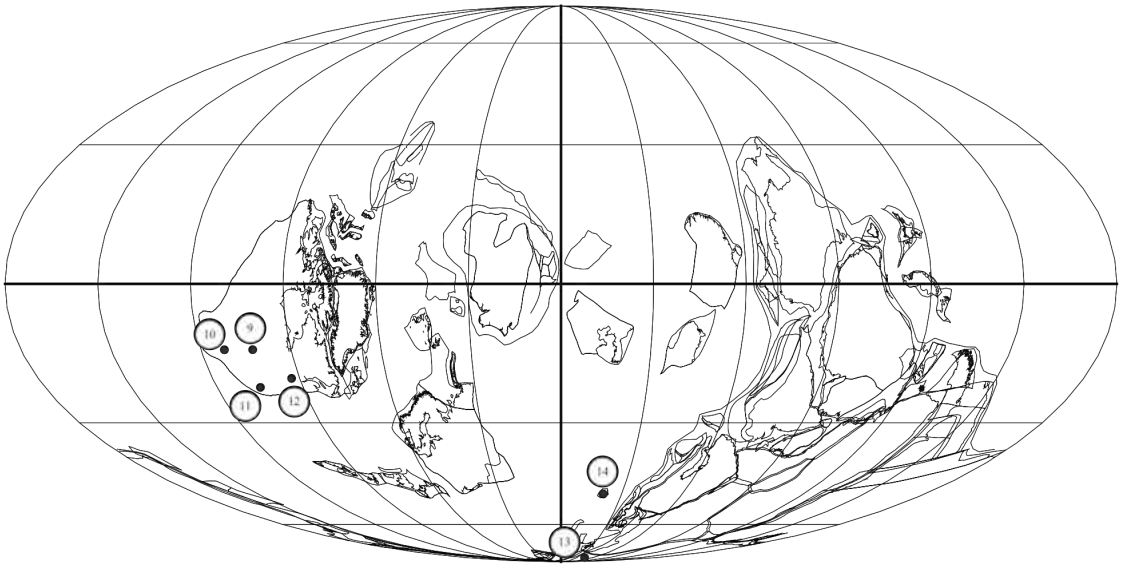
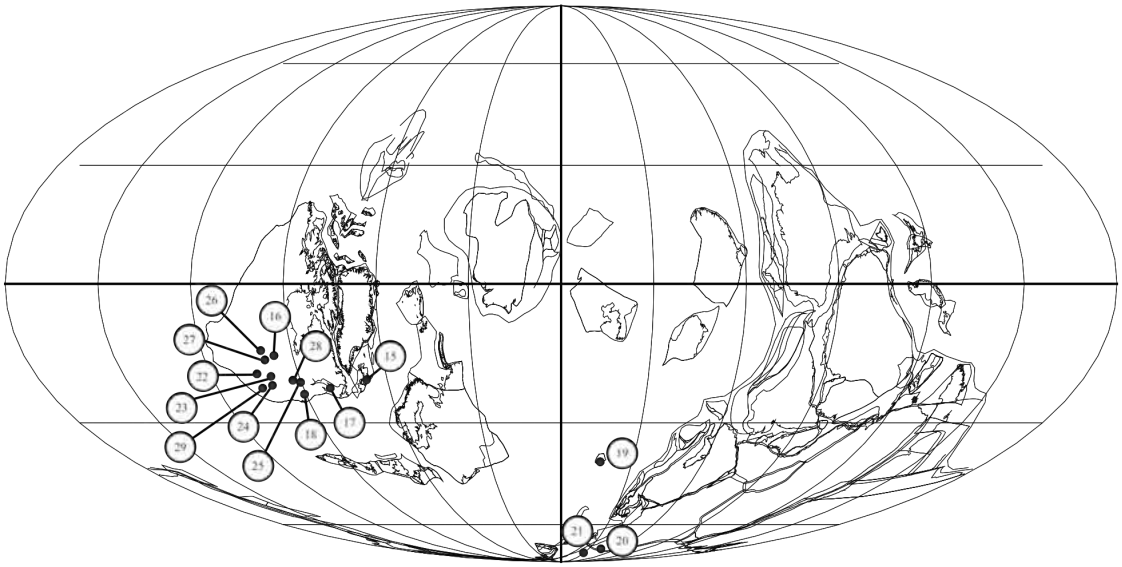


FIGURE IV-9 – Spindle diagram showing increase in diversity throughout the Ordovician. Edrioasteroids gradually increase in diversity through the Early and Middle Ordovician before reaching their diversity peak during the Early-Late Ordovician (Katian). Diversity decreases to one genus during the Hirnantian.



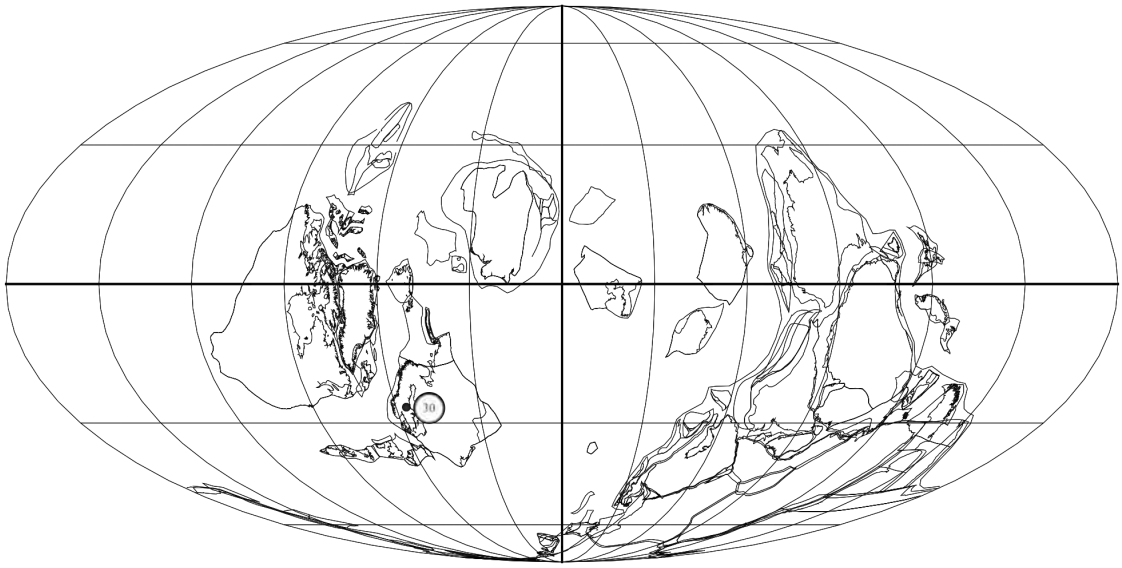
Sandbian (461-455 Ma)

FIGURE IV-10 – Paleogeographic map of the Sandbian. Circles indicate location of known edrioasteroid occurrences. Key can be found in Table 1.



Katian (455-446 Ma)

FIGURE IV-11 – Paleogeographic map of the Katian. Circles indicate location of known edrioasteroid occurrences. Key can be found in Table 1.



Hirnantian (446-444 Ma)

FIGURE IV-12 – Paleogeographic map of the Hirnantian. Circle indicates location of known edrioasteroid occurrences. Key can be found in Table 1.

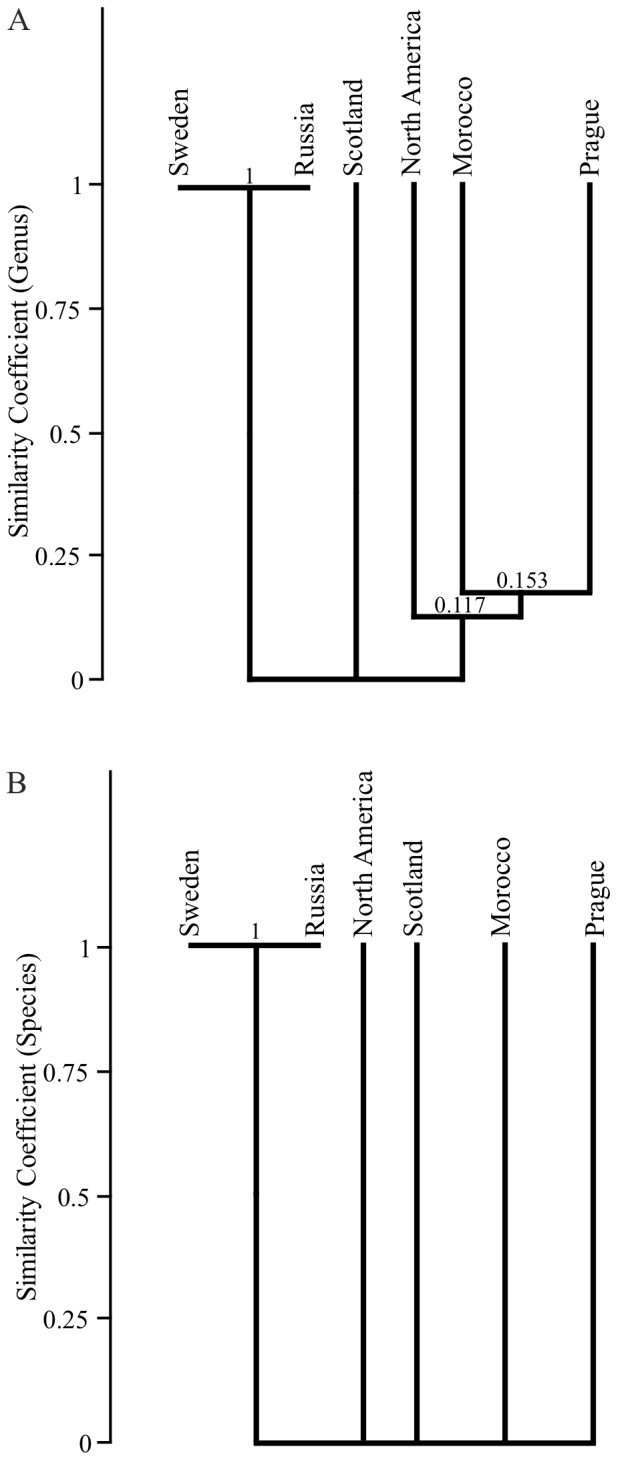


FIGURE IV-13 – Biogeographic dendrograms resulting from cluster analysis. Both show Sweden and Russia are most similar in faunal composition. A) Generic similarity, and B) Species similarity.

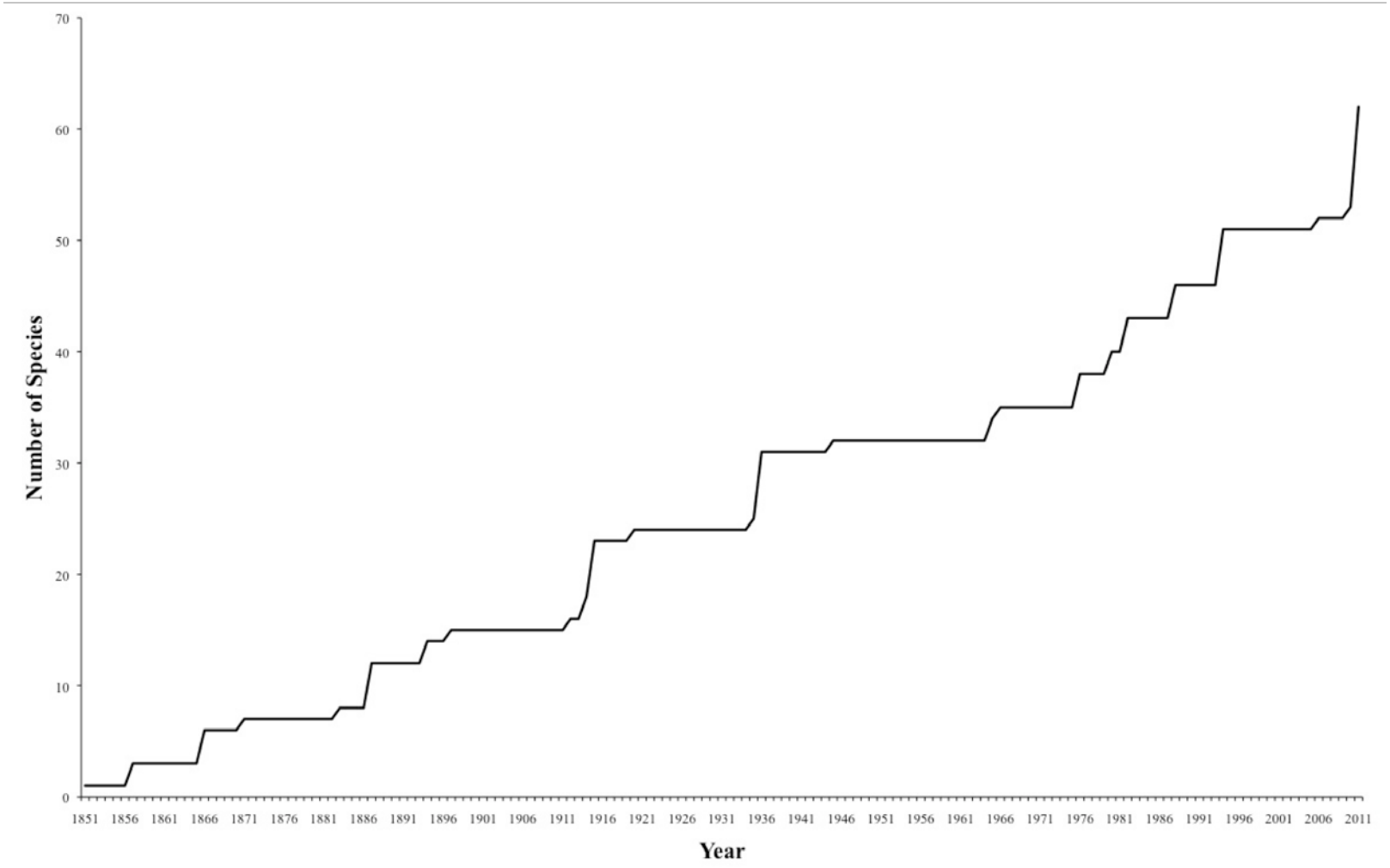


FIGURE IV-14 – Species accumulation curve for all known edrioasteroid occurrences. Increases gradually with few plateaus, yet never reach asymptote, suggesting further fieldwork will enhance diversity.

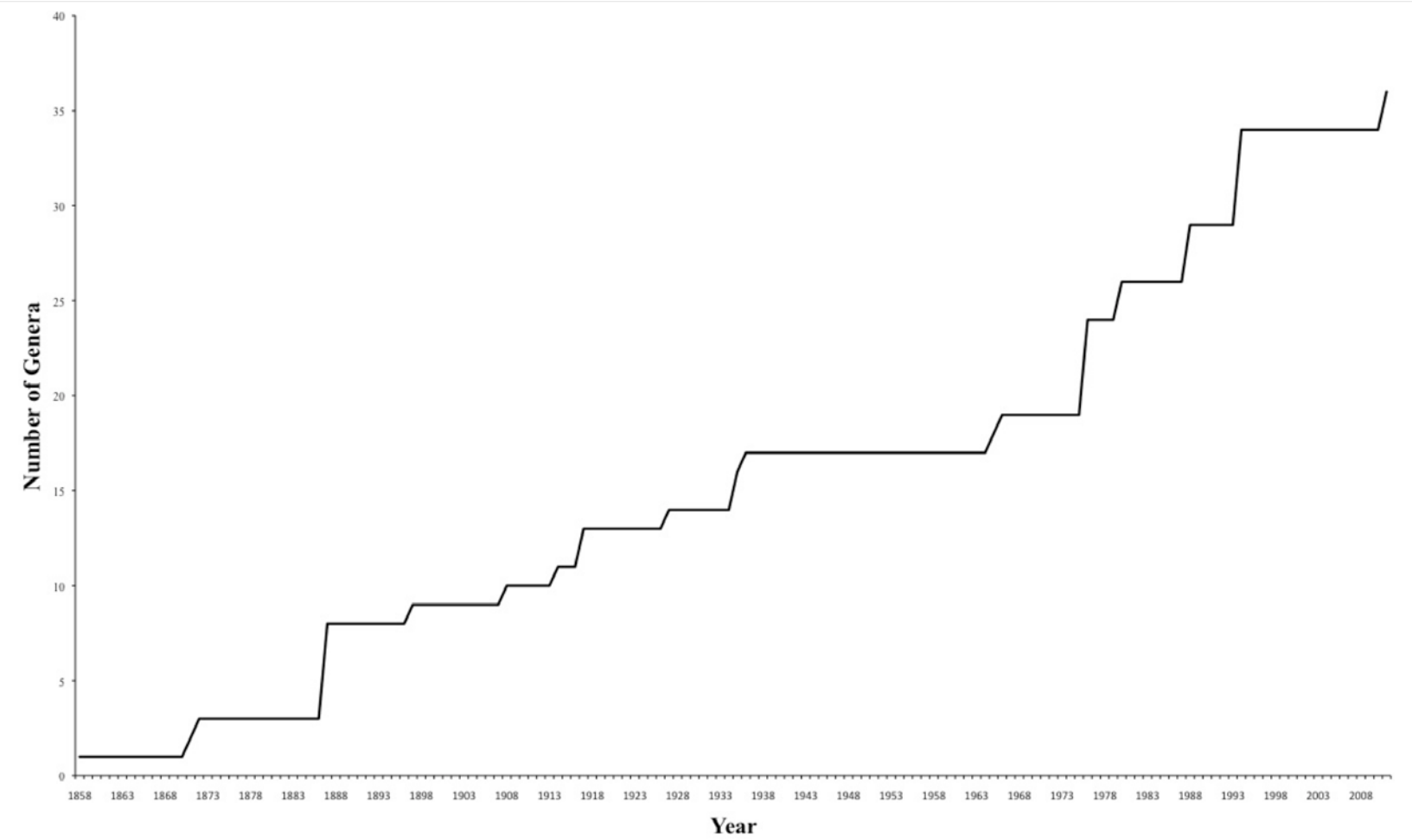


FIGURE IV-15 - Generic accumulation curve for all known edrioasteroid occurrences. Increases gradually with few plateaus, yet never reach asymptote, suggesting further fieldwork will enhance diversity.

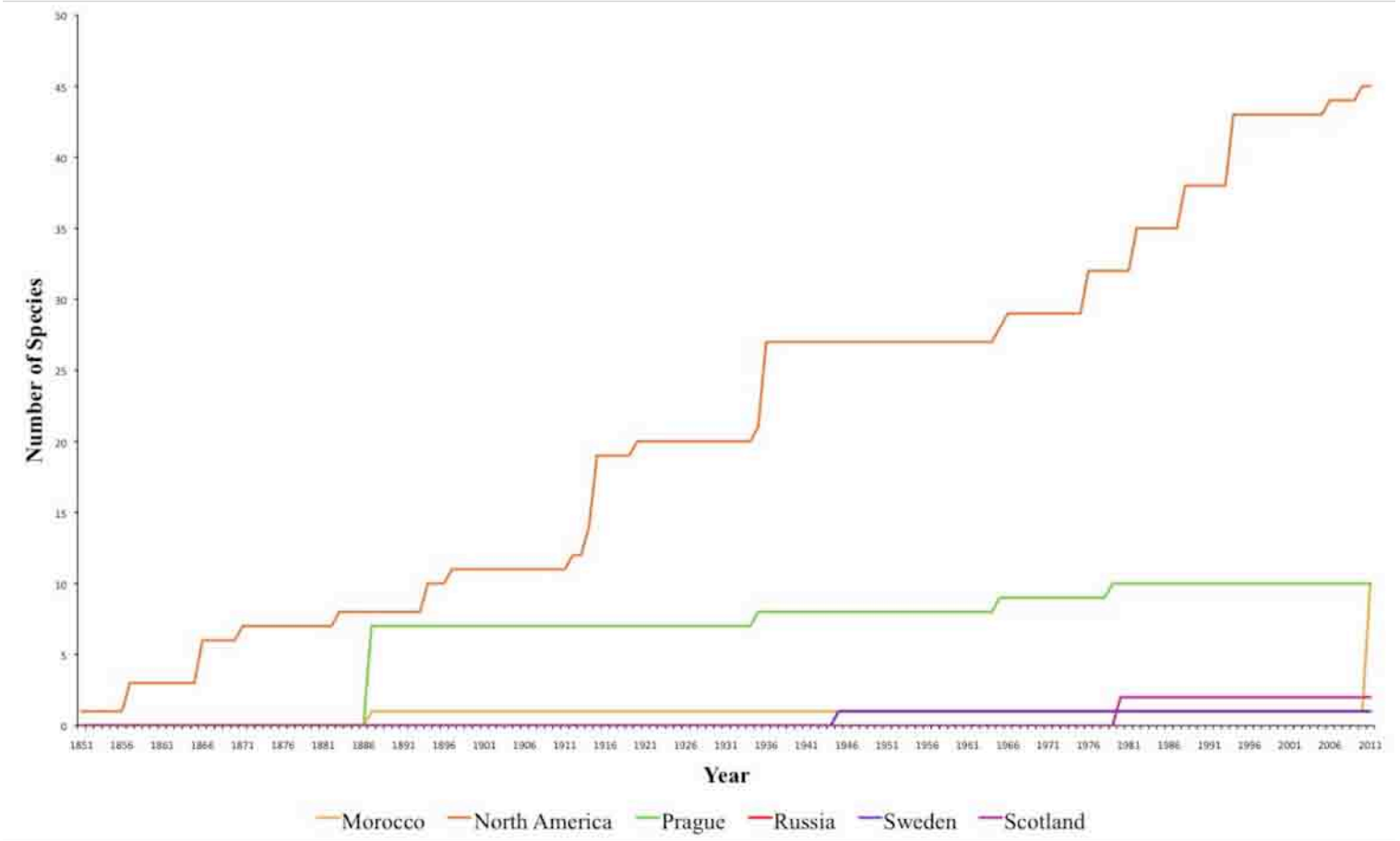


FIGURE IV-16 – Species accumulation curves for edrioasteroids by biogeographic region. North America does not reach asymptote, indicating that further fieldwork will enhance edrioasteroid diversity. Morocco has a sharp spike in diversity from 2010 to present in response to fieldwork by Sumrall and Zamora. Although Prague, Russia, Sweden, and Scotland appear to have reached an asymptote, we suggest this is due to lack of fieldwork, and that additional fieldwork will enhance the diversity record.

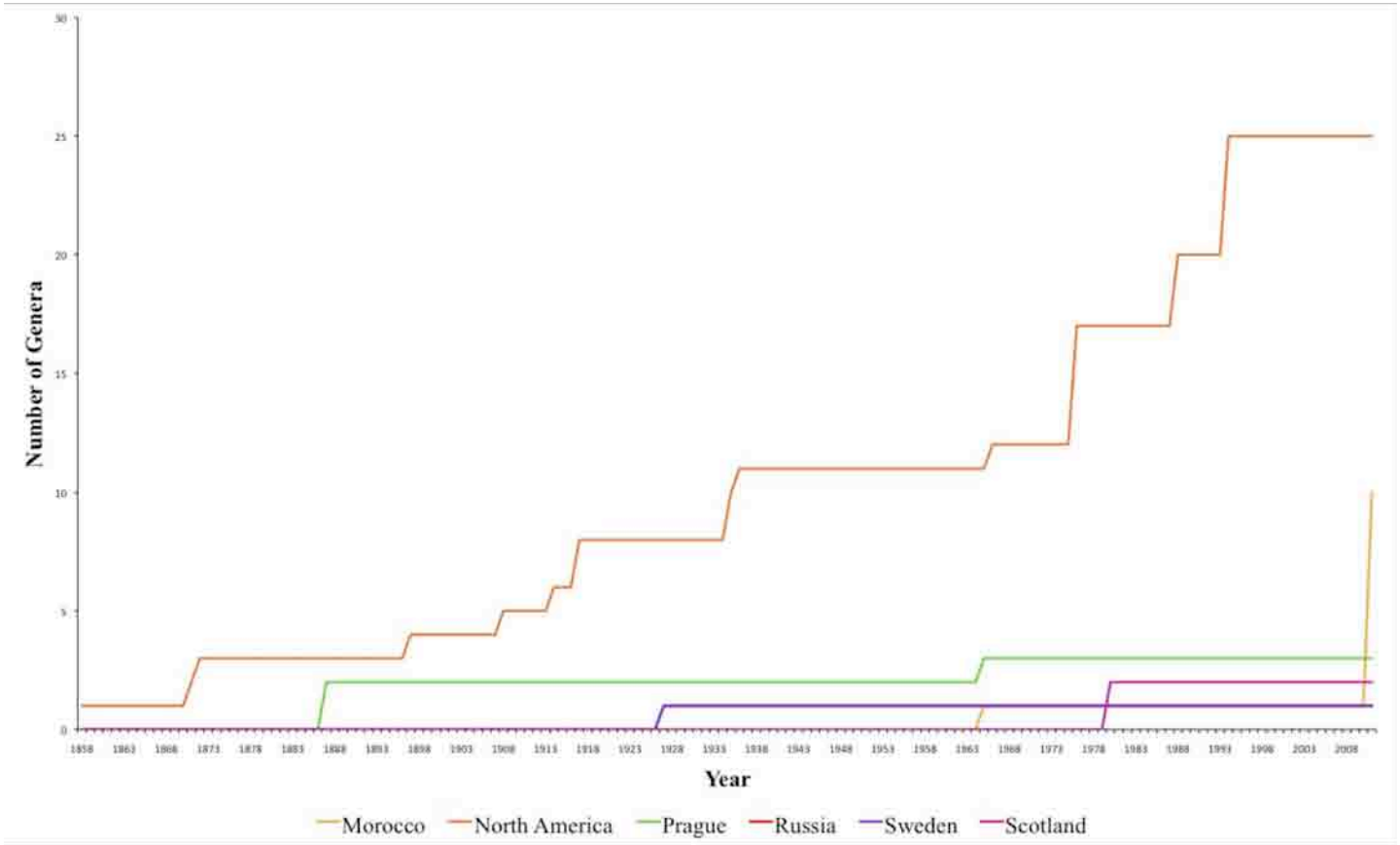


FIGURE IV-17 – Generic accumulation curves for edrioasteroids by biogeographic region. North America does not reach asymptote, indicating that further fieldwork will enhance edrioasteroid diversity. Morocco has a sharp spike in diversity from 2010 to present in response to fieldwork by Sumrall and Zamora. Although Prague, Russia, Sweden, and Scotland appear to have reached an asymptote, we suggest this is due to lack of fieldwork, and that additional fieldwork will enhance the diversity record.

V. CONCLUSIONS

1. Edrioasteroids reached their maximum diversity of 24 genera during the Late Ordovician.
2. Edrioasteroids utilized many forms of hard substrate for settlement including hardgrounds, shell pavements, and living fauna.
3. Edrioasteroid encrustation on the underside of a bryozoan ledge suggests a broader attachment strategy than previously thought.
4. Edrioasteroid density is low on the three examined hard substrates in this study with less than 28 individuals per square meter when compared with other studies that saw a peak of 5,000 individuals per square meter.
5. Histograms of edrioasteroid thecal diameter show various patterns suggesting genera exhibited different breeding and recruitment strategies in different environments.
6. Right-skewed distributions of *Isorophus cincinnatiensis* on the Florence and Sharonville pavements suggest an r-strategist lifestyle with low juvenile survivorship.
7. Generally, edrioasteroids show no preferred orientation on the substrates examined in this study. However, weak thecal orientation was shown for specimens of *Isorophus cincinnatiensis* on the Florence pavement suggesting alignment to the prevailing current.
8. Nearest Neighbor Analysis showed edrioasteroid specimens are generally clustered on the substrate suggesting encrustation in areas with steady current, increased food availability, and improved reproductive success.

9. Species specific variation in edrioasteroid ambulacral width suggests partitioning of food supply.
10. Edrioasteroid marginal deformation and bryozoan overgrowth suggests edrioasteroids were incapable of movement once attached to the substrate.
11. High taphonomic grade suggests either exposure on the seafloor without protection of sediment cover or bloating and rupturing of the theca during the decay process.
12. Biogeographic patterns show that high diversity and population density of Ordovician edrioasteroids are not restricted to warm, tropical waters as was previously thought, rather high diversity and specimen density are also found in the polar regions.
13. New genera recently described from Morocco indicate that additional fieldwork in depauperate areas will likely enhance the faunal record in previously unsampled areas.

VITA

René Anne Shroat-Lewis was born in New York City in August 1964. Her family moved to West Palm Beach, Florida while she was an infant. Raised by her grandparents, William and Irene Martin, René had a very happy childhood. Some of her favorite memories are of fishing with her grandparents in a small town called Jensen Beach, Florida.

René graduated in 1981 from John I. Leonard High School and joined the United States Navy as a Gunners Mate. While in the Navy, she married and had two children, William Christopher and Richard Wayne. After serving 4 years active duty, René was Honorably Discharged and lived throughout southern California, including Long Beach, San Diego, and Camarillo.

In 1997, René moved to Wilmington, North Carolina to be closer to her family. While attending Cape Fear Community College she took a geology course and decided she could mix marine biology with geology. René, the first person in her family to attend university, earned her Bachelor of Science in Geology in 2005 and her Master of Science in Geology in 2007, both from the University of North Carolina Wilmington. After completing her Master's thesis, René moved to Knoxville, Tennessee to pursue a doctoral degree in the Department of Earth and Planetary Sciences at the University of Tennessee.

René is the recipient of many distinguished awards including: The Association for Women Geoscientists Winifred Goldring Award; The Association for Women Geoscientists Chrysalis Scholarship; and the Association for Applied Paleontological Sciences James R. Welch Scholarship.

René is a member of the Geological Society of America, Association for Women Geoscientists, The Paleontological Society, and Sigma Xi.

In her spare time, René is an avid scrapbook artist. To date she has completed over 50 scrapbooks with many more in the works. She won several blue ribbons and one Best of Show in the Tennessee Valley Fair for her work. She enjoys traveling, riding roller coasters and watching chick-flicks, especially those with Colin Firth, who she thinks is the most perfect man on Earth. However, nothing compares to the amount of joy she gets from spending time with her sons, who luckily, also love traveling and riding roller coasters (although they're not really fans of chick-flicks).

René will be moving to Willimantic, Connecticut to begin her new life as a Visiting Assistant Professor at Eastern Connecticut State University.

Finally, one of René's favorite television shows is "Inside the Actors Studio" and has thoughtfully considered her answers to the Pivot Questionnaire. Here they are, for your enjoyment.

1. What is your favorite word? Zooxanthellae
2. What is your least favorite word? Can't
3. What turns you on creatively, spiritually, or emotionally? Laughter/humor
4. What turns you off? Narcissism
5. What is your favorite curse word? Shit
6. What sound or noise do you love? My son's voices
7. What sound or noise do you hate? The dentist's drill

8. What profession other than your own would you like to attempt? Marine biologist
9. What profession would you not like to do? Lawyer
10. If Heaven exists, what would you like God to say when you arrive at the Pearly Gates? Your boys will be fine. It's time to stop worrying.